Annals
of the
Missouri Botanical
Garden

Volume XLIX — L1

1962 — 64

Published quarterly by the Board of Trustees of the Missouri Botanical Garden
and Washington University Press, St. Louis, Mo.

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A quarterly journal containing scientific contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Beginning with Volume 45, 1958:

Subscription Price	$15.00 per volume
Single Numbers	4.00 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., will become sole agent for Annals of the Missouri Botanical Garden. The Agency will handle all subscriptions, all claims (beginning with volume 50 (1963) and all requests for back issues. Out-of-print numbers will be reprinted as may be required.

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PUBLISHED QUARTERLY BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI

Entered as second-class matter at the post-office at St. Louis, Missouri,
under the Act of March 3, 1879.

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Information

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Beginning with Volume 45, 1958:

Subscription Price	$12.00 per volume
Single Numbers	3.00 each

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Vol. XLIX February and May, 1962 No. 1 and 2

STUDIES IN NEW WORLD MORACEAE: TROPHIS, CLARISIA, ACANTHINOPHYLLUM*

WILLIAM C. BURGER

Abstract

This study includes revisions of three New World genera of the family Moraceae which have often been mistaken for one another. Two have been considered synonymous. *Trophis*, has never been the subject of monographic study, but *Clarisia* and *Acanthinophyllum* were revised by Lanjouw in 1936, who treated them as a single genus. In herbaria, critical specimens of one genus have frequently been filed with those of one of the other genera, and new species have occasionally been assigned to the wrong genus. Studying the genera together has permitted a consideration of their relationships and made available misplaced collections.

The revisions are based upon the study of herbarium specimens from seventeen important herbaria of the world. These collections include most of the type specimens of the species, subspecies, and varieties treated.

The study includes discussions of the important morphological characteristics of the genera; relationships of the genera are also briefly discussed. The genus *Sorocea* is included in the discussions.

Four species are recognized in the genus *Trophis*. *Clarisia* and *Acanthinophyllum* are treated as separate genera, each with two species. The subspecies of *T. racemosa* and *C. biflora* and the species of *Acanthinophyllum* are new combinations. WILLIAM C. BURGER, Imperial Ethiopian College, Box 138, Dire Dawa, Ethiopia.

Introduction

This study originally included a revision of the genus *Sorocea*. Only after material had been received from a number of herbaria and the study was well under way did I come to know that Professor J. Lanjouw had been studying *Sorocea* for many years. In July 1961 I had the good fortune of meeting Professor Lanjouw and his assistant Mr. Wessels Boer while visiting Utrecht. There we discussed *Sorocea* and found that our delimitation of species was very similar. We hope to publish a revision jointly in the near future. *Sorocea* is discussed in the following pages and included in a key to the genera.

The genera considered in this study are distinguished from most other dioecious New World Moraceae by their racemose, spicate, or occasionally capitate inflorescences. The pistillate perianth, with rare exceptions, is fused and tubular, while the alternate leaves are distichous and pinnately veined on unarmed branches. *Trophis* has never been monographed, but *Clarisia* and *Acanthinophyllum* were revised by Lanjouw in 1936. The vegetative resemblance and similar flowers and inflorescences of these genera have resulted in numerous misidentifications. Fre-

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* Part of an investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

quently critical specimens of one genus have been filed with those of one of the other genera, and new species have occasionally been assigned to the wrong genus. Thus, *Trophis macrostachya*, and nearly all the specimens which were referred to it, belong with *Sorocea*. Lanjouw concluded that *Clarisia* and *Acanthinophyllum* are congeneric and it has been suggested more recently (Woodson, 1960, p. 114) that *Trophis* and *Sorocea* might be congeneric. Studying the genera together has permitted a consideration of their relationships and made available misplaced collections which would not have been possible had only one genus been studied.

Inflorescences

The staminate inflorescences are racemose or spicate, or condensed into small capitula in several species of *Sorocea*. These inflorescences are most commonly paired in the axils of leaves. In *Trophis* there is a reduction to solitary inflorescences in *T. chiapensis*. The spikes of *Clarisia* and *Acanthinophyllum* are especially interesting in that the stamens arise directly from the rachis and the tetramerous organization of tepals and stamens has been lost. The most elaborate type of inflorescence found among the genera studied is that of *Clarisia racemosa*. These "racemes" of staminate spikes are interpreted as leafless flowering shoots and are discussed in more detail under the special remarks on that genus.

The pistillate inflorescences parallel the staminate in *Trophis* and *Sorocea*. The pistillate flowers of *Clarisia* may be the result of a similar reduction. The peltate bracts at the base of the receptacle and the paired, axillary flowers of *C. biflora* may be interpreted as evidence for such a reduction. As in the staminate spikes the development of leafless flowering shoots has apparently resulted in the elongate pistillate "racemes" of *C. racemosa*. The pistillate capitula of *Acanthinophyllum* resemble those found in some species of *Sorocea* but are distinguished by the uncinate trichomes of the peduncle and the paucity of bracts subtending the flowers.

The nature and origin of the spikes and racemes, characteristic of the genera under consideration, remain hypothetical. Bernbeck (1932), in an important morphological study, concluded that the inflorescences of Urticaceae and Moraceae are basically cymose. The spikes and racemes that I have seen are noteworthy in usually lacking flowers along one or sometimes two sides of the inflorescence and thus simulating helicoid cymes. This is similar to the inflorescences of *Myriocarpa cordifolia* and *Urtica membranacea* studied by Bernbeck and interpreted by him to be derived from a cymose type. While Bernbeck did not study Moraceae with inflorescences of the type found in the genera under discussion, it seems safe to assume that they, too, arose from a cymose type.

Staminate Flowers

The staminate flowers fall into two categories: those that are definitely organized and tetramerous and those where the organization has been lost and the flowers are reduced to single stamens. The tetramerous flowers are readily distinguishable in *Trophis* and *Sorocea*. The stamens are inflexed before anthesis and the perianth is valvate in aestivation in *Trophis*, while the stamens are straight and

the perianth is decussate-imbricate in *Sorocea.* Dehiscence of the anthers is introrse in *Trophis,* but is usually extrorse in *Sorocea*; a pistillode is always present in *Trophis,* but is rare in *Sorocea.* These distinctive characteristics clearly serve to separate the two genera despite the similarity of the pistillate flowers.

The reduced flowers of *Clarisia* and *Acanthinophyllum,* lacking a definite perianth, are more difficult to distinguish. The stamens of both genera are straight before anthesis, but the anthers of *Clarisia* are subbasifixed while those of *Acanthinophyllum* are usually dorsifixed. The smaller size of the anthers (ca. 0.3 mm.) and the retrorse uncinate trichomes of the peduncle further distinguish *Acanthinophyllum.* I believe that the reduction of the staminate flowers in these two genera does not reflect a true relationship but rather a parallel evolution. Without intermediate stages or morphogenetic studies it is not possible to indicate how this reduction took place. Woodson (1960, p. 125) has described an interesting series among several species in *Brosimum* where there is a gradual reduction in stamen number and a striking change in the mode of dehiscence. However there may be another way in which the staminate flowers became reduced. This would require that the flowers first became broadly sessile with the stamens and perianth parts arising separately from the rachis as in some species of *Sorocea.* Following this, reduction in the perianth parts together with a loss of symmetry might give rise to spikes such as are found in *Clarisia* and *Acanthinophyllum.*

Pistillate Flowers

The pistillate flowers of the four genera under discussion are very similar. This is not unexpected since the basic plan of the gynoecium is quite uniform in the Urticales. The fusion of perianth parts of the pistillate flower is frequent in Moraceae and is not in itself indicative of close relationship. I have placed some emphasis on the length and form of the style branches which would separate *Trophis* and *Clarisia* from *Sorocea* and *Acanthinophyllum.* The short style branches and free perianth tube of *Acanthinophyllum* ally it to *Sorocea* rather than to *Clarisia,* with which it had been made congeneric by Lanjouw. The fruit of the genera are quite similar, but the embryo of *Sorocea* may be separated on the basis of its fused cotyledons and prominent hypocotyl 2-3 mm. long. The cotyledons of the other genera are free and the hypocotyl is minute.

Anatomical Characters

The trichomes, while often not consistent among all the species of a genus, may nevertheless be useful in suggesting relationships with other genera. *Sorocea,* for example, usually possesses minute (0.05 mm.) multicellular gland-tipped trichomes. Though species of *Sorocea* in Central America may lack these trichomes, I believe it is significant that they are not found in any of the other genera studied. *Acanthinophyllum* can be immediately distinguished from the other genera under consideration by its small (0.1 mm.) retrorse uncinate trichomes. The leaf surfaces of *Trophis* can be distinguished from other genera by the minute (0.02 mm.) broadly aculeiform trichomes bordered by about a dozen small epidermal cells. These trichomes are numerous in the usually scabrous leaves of *T. racemosa* but

sparse in the other species. *Clarisia* lacks distinguishing trichomes that might serve to aid in its placement.

The epidermal cells of *Acanthinophyllum* have a deeply sinuate outline unlike those of the other genera. These and the smaller trichomes can be seen on dried herbarium specimens under low power of the compound microscope by reflected light; clearing is unnecessary.

Relationships of the Genera

The subfamilies Moroideae and Artocarpoideae have been defined on the basis of whether the stamens are inflexed or straight in bud. As a result, *Trophis* has been placed in the Moroideae and *Clarisia, Acanthinophyllum,* and *Sorocea* in the Artocarpoideae. These subfamilies also have been divided on the basis of leaf vernation. The Moroideae have conduplicate leaf vernation while the Artocarpoideae have involute leaves. *Clarisia* has conduplicate leaf vernation but straight stamen aestivation, a contradiction of the subfamilial criteria. If the staminate flowers have become disorganized there is no reason to assume the orientation of the stamens could not change radically. I believe that the criterion of staminal position prior to anthesis cannot be critically applied to such reduced forms as *Clarisia* and that other characters must be sought in determining relationships.

Inflorescence type has been used in classification at the tribal level. In *Sorocea* and *Clarisia,* however, the inflorescences are quite variable and anatomical criteria may prove more important in determining generic relationships. In the absence of a modern study of the family it is not possible to define the relationships of the four genera under discussion. The short remarks that follow indicate what I believe to be their affinities.

Trophis, with the stamens inflexed in bud, is clearly a member of the Moroideae related to *Paratrophis* of the western Pacific. The valvate aestivation of the staminate flowers and consistently tubular perianth in the pistillate flowers separate *Trophis* from *Paratrophis* despite the fact that *P. philippinensis* has a tubular pistillate perianth very similar to that of *Trophis.*

Clarisia, with long slender style branches and subbasifixed anthers, resembles *Trophis* more closely than the other genera I have studied. This would imply that the stamens were originally inflexed in bud and agrees with the fact that the leaves are conduplicate in bud; a characteristic of the subfamily Moroideae. I would therefore transfer *Clarisia* from the subfamily Artocarpoideae to the Moroideae and place it near *Trophis* among New World genera.

Acanthinophyllum was considered congeneric with *Clarisia* by Lanjouw but I believe that actually they are not closely related. The short-styled pistillate flowers with free perianth tube resemble those of *Sorocea.* The retrorse uncinate trichomes and sinuate epidermal cells are also found in *Trymatococcus* of the Moroideae and *Helianthostylis* of the Artocarpoideae among American genera. On the basis of the characters of the pistillate flowers I would retain *Acanthinophyllum* in the Artocarpoideae and place it near *Helianthostylis.*

Sorocea is clearly referable to the Artocarpoideae where it was placed in the fundamental study of Trécul (1847) and with which later investigators have con-

curred. Inasmuch as the New World Artocarpoideae are in need of a thorough general study there is no point to suggesting a change in the placement of *Sorocea* by Engler in "Das natürlichen Pflanzenfamilien" which was based on the work of Bentham and Hooker (1880).

Illustrations

The illustrations are my own. The foliage is nearly half natural size while the staminate and pistillate flowers are about 8x. The inflorescences with young fruit are reproduced at a magnification of about 4x.

Materials

This study is based on specimens from the following herbaria. The abbreviations are taken from Lanjouw & Stafleu's 'Index Herbariorum,' Part 1 (Regnum Vegetabile vol. 15, 4th edition, 1959).

A—Arnold Arboretum, Harvard University, Cambridge
B—Botanisches Museum, Berlin-Dahlem
BM—British Museum, London
C—Botanical Museum and Herbarium, Copenhagen
F—Chicago Natural History Museum, Chicago
GH—Gray Herbarium of Harvard University, Cambridge
LIL—Instituto Miguel Lillo, Tucumán
MEXU—Herbario Nacional del Instituto de Biología, Mexico
MG—Museu Paraense Emilio Goeldi, Belem
MICH—University Herbarium, University of Michigan, Ann Arbor
MO—Missouri Botanical Garden, Saint Louis
NY—New York Botanical Garden, New York
P—Muséum National d'Histoire Naturelle, Paris
PB—Jardim Botânico, Rio de Janeiro
S—Botanical Department, Naturhistoriska Riksmuseum, Stockholm
US—U. S. National Museum, Smithsonian Institution, Washington
Y—Yale School of Forestry, New Haven

I am indebted to the curators of these herbaria for the loan of specimens which included many valuable types. I also wish to thank Dr. George Van Schaack for assistance in the use of the library of the Missouri Botanical Garden. I am especially indebted to Professor Robert E. Woodson, Jr., for suggesting this study and for his advice and guidance throughout the course of its completion.

Key to the Genera

A. Cotyledons distinct in the seed; staminate flowers tetramerous with valvate aestivation or not definitely organized; lacking multicellular gland-tipped trichomes on the leaves ..... B
B. Anthers 0.5 mm. long or longer; pistillate flowers with long slender style branches; peduncles lacking minute retrorse uncinate trichomes; leaves conduplicate in bud, midvein impressed above C
C. Staminate flowers tetramerous, the tepals valvate and the stamens inflexed in aestivation; pistillate flowers sessile or if pedicellate lacking bracts at the base of the receptacle ..... I Trophis
CC. Staminate flowers not definitely organized; pistillate flowers pedicellate with peltate bracts at the base of the receptacle ..... II Clarisia

BB. Anthers 0.2—.03 mm. long the staminate flowers not definitely organized; pistillate flowers with short broad style branches; peduncles densely invested with minute (0.1 mm.) retrorse uncinate trichomes; leaves involute in bud, the midvein prominulous .....III Acanthinophyllum

AA. Cotyledons fused in the seed; style branches usually short and broad; staminate flowers tetramerous, the tepals decussate-imbricate and the stamens straight in aestivation; leaves involute in bud, multicellular gland-tipped trichomes usually present on the leaves, midvein impressed above .....IV Sorocea

Taxonomy

I. TROPHIS P. Br.

Trophis P. Br. Hist. Jamaica 357. 1756, nom. conserv. [T.: *T. Americana* L. = *T. racemosa* (L.) Urb.]

Bucephalon L. Sp. Pl. 1190. 1753, nom. rejic. [T.: *B. racemosum* L.]

Skutchia Pax & Hoffm. ex Morton, in Journ. Wash. Acad. Sci. 27: 306. 1937. [T.: *S. caudata* Pax & Hoffm.]

Dioecious laticiferous unarmed shrubs and trees. Leaves alternate, distichous, bistipulate, pinnately veined, the petioles sulcate above. Stipules lateral, caducous or occasionally persistent, their scars encircling less than half the stem. Inflorescences axillary on the leafy stems, paired or solitary, racemose or spicate, with triangular or suborbicular bracts along the rachis. Flowers unisexual, regular and basically tetramerous, usually lacking along one side of the inflorescence. Staminate flowers: sessile or pedicellate; perianth 4-parted or 4-lobed, the tepals equal and valvate; stamens 4, antetepalous, strongly inflexed in the bud but erect at anthesis, filaments slender and glabrous, the anthers subcentral with 2 somewhat divergent thecae, dehiscing longitudinally, introrse; pistillode always present, cylindrical to rectangular, puberulent. Pistillate flowers: sessile or pedicellate, the perianth tubular, irregularly or minutely 4-lobed at the apex; pistil 1, the ovary superior to inferior by adnation of the perianth tube, 2-carpellate, unilocular, the ovule solitary, anatropous and pendulous from below the apex of the locule, the style deeply bifid, the style branches long and slender with the inner stigmatic surface densely and minutely papillate. Fruit drupaceous, the perianth tube accrescent and succulent, the stone globose, the embryo large and straight with thick equal cotyledons and minute hypocotyl, without endosperm.

The genus was first recorded by Plumier in 1703 (Nova Plant. Amer. Gen. p. 52) as *Bucephalon* and this was adopted by Linnaeus in his Genera Plantarum (1737) and Species Plantarum (1753). However, preferring a more adequate description, Linnaeus later (Systema Naturae ed. 10, p. 1289. 1759) chose to use the name *Trophis* described by Patrick Browne in 1756 (p. 357). Usage has concurred with Linnaeus and has led to the conservation of *Trophis*. The name is derived from the Greek word τροφή (nourishment) referring to its frequent use as forage.

Trophis has not received monographic study since Bureau's treatment of the Moraceae in De Candolle's 'Prodromus' (1873) and although the species are rather closely knit, their identification is usually not difficult. Determining a phylogenetic sequence for the four species, however, is a somewhat conjectural matter. I have begun the sequence with *T. racemosa*, in some respects the most specialized species. *T. racemosa* rejoys a much wider distribution, has adapted to a greater range of habitats, and possesses greater morphological variation than is found in any other

species. These considerations lead me to suspect that it is the oldest element of the genus. The lack of fusion of the staminate perianth parts corroborates this view, but the usually inferior ovary and condensed inflorescences are definitely advanced. I believe that *Trophis* is closely related to *Paratrophis* of the southwest Pacific in which the pistillate perianth is usually 4-parted and imbricate. In *Paratrophis* the pistillate flowers are broadly sessile, quite similar to *T. racemosa* and the major argument for the antiquity of the latter. If this view is correct, the long pedicels of pistillate flowers and fruit in the other species of *Trophis* are secondarily evolved. The fact that the fruit of *T. racemosa* is never pedicellate while the fruit of the other species are occasionally sessile may indicate that the latter, less stable, condition is derived.

The geographical center of the genus is in southern Mexico where all four species are found.

KEY TO THE SPECIES

a. Pistillate flowers quite sessile and not constricted at the rachis; fruit sessile, densely velutinous; staminate flowers sessile and crowded, the perianth parts essentially free; leaves frequently scabrous on either or both surfaces. Mexico to Peru, Venezuela and the West Indies .....1. T. RACEMOSA

aa. Pistillate flowers pedicellate or rarely subsessile but constricted at the rachis; fruit usually pedicellate, sparsely puberulent to glabrescent; staminate flowers sessile or pedicellate, usually not crowded, the perianth parts connate toward the base; leaves never scabrous.

b. Leaves glabrous or very sparsely puberulent beneath; branchlets slender; pistillate flowers sparsely cinerous-puberulent.

c_4 Staminate flowers, sessile; pistillate inflorescence to 10 cm. long; leaves elliptic to elliptic-oblong or obovate, usually over 3 cm. wide. Mexico to Guatemala .....2. T. MEXICANA

cc. Staminate flowers pedicellate; pistillate inflorescences to 4 cm. long; leaves linear-lanceolate to narrow elliptic, less than 3 cm. wide. Southern Mexico to Guatemala .....3 T. CHIAPENSIS

bb. Leaves persistently short-pilose beneath; branchlets thick; pistillate flowers densely ferrruginous-puberulent. Southern Mexico .....4. T. CUSPIDATA

1. TROPHIS RACEMOSA (L.) Urb. Symb. Ant. 4:195. 1905.

Bucephalon racemosum L. Sp. Pl. 1190. 1753. [T.: Linn. Herb. London (1156.1) (♀ ♂) photo.]

Trophis americana L. Syst. Nat. ed. 10. 1289. 1759.

Shrubs or trees to 18 m. tall, the trunk to 50 cm. in diameter and often divided, with rough brown bark and milky latex; leafy branchlets usually stout, 2.0-3.8 mm. in diameter, hirtellous becoming glabrescent, conspicuously lenticellate on older parts. Leaf blades obovate to oblong or elliptic, 5-23 cm. long, 2.4-10 cm. broad, acuminate to subcaudate-acuminate, obtuse to acute and often slightly oblique at the base, subcoriaceous to membranaceous, often scabrous, glabrous, above and glabrous or minutely strigose beneath, the midvein plane or impressed above, prominent below with 4-8 pairs of ascending secondary veins arching upward near the entire or serrulate, occasionally deeply sinuate margin; petiole 4-16 mm. long, 0.7-2.0 mm. in diameter, minutely puberulent and glabrescent. Stipules caducous or persistent, lanceolate, 2.0-3.8 mm. long, their scars small and inconspicuous. Staminate inflorescences: spicate, paired or solitary in the axils of leaves or rarely of undeveloped or fallen leaves, 1.5-5.0(-7.5) cm. long, the peduncles 1.3-11.0 mm. long, minutely velutinous, the rachis with numerous triangular or suborbicular

peltate or basally attached bracts 0.5-1.1 mm. broad; flowers 15 to many and densely crowded, sessile or rarely subsessile, about 4 mm. long and 4 mm. wide, the perianth parts 1.6-2.2 mm. long, 1.0-1.5 mm. wide, acute or obtuse at the apex, free or basally connate, minutely puberulent, the trichomes about 0.1 mm. long; staminal filaments 2.0-2.6 mm. long, the anthers 0.8-1.2 mm. long; pistillode 0.3-0.6 mm. long. Pistillate inflorescence; spicate, paired or solitary in the axils of leaves or rarely fallen or undeveloped leaves, 1.8-4.0(-6.0) cm. long, the peduncle 1.2-10 (-14) mm. long, minutely velutinous, the rachis with numerous triangular or suborbicular peltate or basally attached bracts 0.5-1.2 mm. broad; flowers 4-15, broadly sessile, ovoid or conic, the perianth tube indistinctly or minutely 4-lobed at the apex, 2.0-4.5 mm. long, 1.4-2.5 mm. in diameter, densely velutinous, the trichomes about 0.1 mm. long, ovary inferior or rarely half-inferior, the style branches slender, 2.0-5.5 mm. long. Fruit globose or ovoid, occasionally with a narrow collar at the apex, about 1 cm. in diameter, smooth or ridged, minutely velutinous, becoming bright red and sometimes blackish.

This species is quite common throughout a range that extends from southern Sonora, Mexico, to eastern Peru and the West Indies. It is found on hillsides and river valleys in Mexico and moist forests in Central and South America. Within this wide area it has begun to differentiate into three morphologically distinct populations which I am recognizing as subspecies. Subspecies *ramon* and *racemosa* with their relatively thick leaves have apparently become adapted to more xeric habitats than ssp. *meridionalis*. The elongate inflorescences and occasionally half-inferior ovaries of ssp. *meridionalis* add to my impression of its more primitive nature. Subspecies *ramon* and *meridionalis* intergrade quite imperceptibly in western Panama and northern Colombia. I have used the Panama-Colombia boundary to separate the two subspecies realizing, of course, that no real discontinuity exists. The membranaceous, serrulate and long-acuminate leaves of most Colombian specimens make their assignment to ssp. *meridionalis* quite natural even though some may have the congested pistillate inflorescences characteristic of ssp. *ramon*.

T. racemosa is closely related to *T. mexicana* with which it is occasionally confused. The densely velutinous fruit and scabrous leaves are diagnostic.

Key to the Subspecies

a. Pistllate inflorescence to 4.5 cm. long at anthesis, the flowers distant, usually more than 1 mm. apart; leaves smooth on both surfaces, tapering to the acuminate apex
  b. Leaves entire, firmly chartaceous to subcoriaceous, acuminate; rachis of the pistillate inflorescence 1.0-1.8 mm. in diameter. West Indies....1c. ssp. RACEMOSA
  bb. Leaves serrulate, membraneous to chartaceous, narrowly acuminate; rachis of the pistillate inflorescence 0.6-1.2 mm. in diameter. Colombia to Peru and Venezuela .....1a. ssp. MERIDIONALIS
aa. Pistillate inflorescences to 2.5 cm. long at anthesis, the flowers crowded, rarely more than 1 mm. apart; leaves scabrous or scabrescent on either or both surfaces, firmly chartaceous to subcoriaceous, usually abruptly short-acuminate. Mexico to Panama .....1b. ssp. RAMON

1a. Trophis racemosa ssp. **meridionalis** (Bur.) W. Burger, comb. & stat. nov.

Trophis americana γ *meridionalis* Bur. in DC Prodr. 17: 253. 1873. [T.: *Bonpland 1512* (P) (♂)]

Sorocea colombiana Standl. in Trop. Woods, no. 19: 39. 1929. [T.: *Curran 186* (F) (♀)]

Trophis racemosa var. *meridionalis* (Bur.) Macbr. in Field Mus. Pub. Bot. 13²: 308. 1937.

Figure 1. *Trophis racemosa.* ssp. *meridionalis:* from *Killip* 35580 (1 [upper right] & 2). ssp. *ramon:* from *Burger 148* (3). ssp. *racemosa:* from *Harris 10858* (4).

Leaf blades elliptic to elliptic-oblong, (5.0-) 7.5-19.0 cm. long 2.5-6.5 cm. broad, gradually tapering to a long and narrowly acuminate apex, acute to obtuse at the base, membranaceous to chartaceous, smooth on both surfaces, glabrous, the margin serrulate. Staminate inflorescences: 2.5-6.0 cm. long, the flowers numerous and densely crowded or rarely somewhat distant. Pistillate inflorescences: 1.5-4.5 cm. long, the rachis 0.6-1.2 mm. in diameter, the pistillate flowers usually more than 1 mm. distant along the rachis.

Flowering from late October through February and May to June. Moist forests and river valleys from sea level to altitudes of 1000 meters.

Vernacular names: *Uspai-manchinga* (Peru-Ll. Williams); *Marfil* (Venezuela-Pittier).

Colombia: Bolívar: San Martín de Loba and vicinity, *Curran 102* [(♂) US], *186* [(♀) F, US], *205* [(♀) S, US], 372 [(♀) US]. caquetá: Solano, 7 km. SE of Tres Esquinas, *Little & Little 9670* [(♂) US]. cauca: Noanamite, Río Micay, *Cuatrecasas 14227* [(♀) A]. chocó: Bahia de solano; *Fernandez 310* [(♂) US] bank of of Río San Juan, near Andagoya, *Killip 35392* [(♀) F, US]. valle del cauca: La Trojita, Río Calima, *Cuatrecasas 16348* [(♂) F], *16810* [(♀) F], Cisneros, *Killip 35580* [(♂) BM, F, S, US]; goajira: 12 km. S. of Carraipia, *Haught 4224* [(♂) F. US]. putumayo: La Concepción, *Cautrecasas 10840* [(♂) F, US]. santa marta: *H. H. Smith 1752* [F (♀), MO (♂), P (♂), S (♂), US (♂)], 2732 [(♂) BM, F, MO, S, US]. sur de santander: vicinity of Puerto Berrio, *Haught 1864* [(♂) F, US]. without precise locality: ad Fluvium Magdalenam, *Bonpland 1512* [F (?), P (♂)]; *mutis* 2992 [(♀) F].

Venezuela: aragua: Patanemo Valley, *Pittier 8659* [(♂) NY, US]; Parque Nacional, *Ll. Williams 10719* [(♀) F].

Ecuador: napo-pastaza: Tena. *Asplund 9387* [(♀) NY, P]; Tiputini-Lagarto Cocha, *Fagerlind & Wibom 2376* [(♀) S], *2403* [(♀) S]; Chimbo River valley, *Rimbach 187* [(♀) F, NY, S].

Peru: amazonas: Aramango, *Woytkowski 5645* [(♀) MO]. huanuco: Tingo María, *Stork & Horton* 9506 [(♂) F]. loreto: Yurimaguas, lower Río Huallaga, *Killip & Smith 27685* [(♀) F]; Florida, Río Putumayo, *Klug 20709* [(♂) BM, F, MO, S]; above Pongo de Manseriche, *Mexía 6282* [(♂) BM, F, LIL, MICH, MO, S], 6303 [(♀) BM, F, LIL, MICH, MO, S]; Santiago-Mundung am Pongo de Manseriche, *Tessmann 4083* [(♀) S]; lower Río Huallaga, *Ll. Williams 4658* [(♀) F], san martín: Juanjui, Alto Río Huallaga, *Klug 3794* [(♂) BM, F, MO, S]; near Tarapoto, *Spruce 4521* [(♀) B, BM], *Ule 6838* [(♀) MG], *Ll. Williams 6542* [(♀) F], 6573 [(♀) F].

1b. Trophis racemosa ssp. **ramon** (Schlecht. & Cham.) W. Burger, comb. & stat. nov.

Trophis Ramon Schlecht. & Cham. Linnaea 6: 357. 1831. [T.: *Scheide & Deppe s.n.* near Misantla (B no. 6750) (♀)].

Trophis americana β. *Ramon* Bur. in DC Prodr. 17: 253. 1873.

Sahagunia urophylla Donn. Sm. in Bot. Gaz. 40: 11, 1905. [T.: *Wilson 54* (US) (♀)].

Clarisia urophylla (Donn. Sm.) Lanj. in Rec. Trav. Bot. Néerl. 33: 263. 1936.

Leaf blades obovate to elliptic-oblong, ovate or elliptic, 5.0-23 cm. long, 2.5-10 cm. wide, short-acuminate to subcaudate-acuminate or rarely tapering to a long-acuminate apex, obtuse or occasionally acute at the base, subcoriaceous to thickly chartaceous, scabrous or scabrescent, glabrous above and glabrous or minutely strigose beneath, the margin entire or occasionally serrulate, the new shoots often with deeply sinuate leaves. Staminate inflorescence: 1.2-4.0(-5.8) cm. long, the staminate flowers densely crowded. Pistillate inflorescences: 0.6-1.8(2.7) cm. long at anthesis, the flowers densely clustered or closely approximate, the rachis 0.8-2.0 mm. in diameter.

The scabrescent, pergamentaceous leaves and congested inflorescences are appar-

ently associated with an adaptation to more xeric conditions than those tolerated by other members of the genus. This is the only subspecies of *T. racemosa* sympatric with other species of the genus.

Dry hillsides, ravines, river valleys and forests; flowering intermittently throughout the year, from sea level to 2500 m. altitude.

Vernacular names: *Ramón* (Mexico to Panama); *Capomillo* (Mexico-Ortega); *Ushi* (Mexico-Mexía); *Cha cox* (Mexico-Flores); White ramon, *Ramón colorado, Yaxox* (British Honduras-Lundell); *Ojushte* (El Salvador-Standley); *Ujushte* (El Salvador-Calderón); *Hoja tinta* (Honduras-von Hagen); Breadnut, *Ojoche macho* (Panama-Cooper & Slater).

MEXICO: CHIAPAS: Escuintla: *Matuda 2598* [(♀) F, MICH], *4022* [(♀) MICH, MO], Esperanza, *Matuda 16794* [(♀) F], La Grada, *Matuda 16799* [(♂) F]; S. Terena Acapatahua, *Matuda 16751* [(♂) F, MICH]. COLIMA: Coahuayana, *Emrick 133* [(♂) F]. GUERRERO: San Antonio, Montes de Oca, *Hinton 11540* [(♂) F, US]; Temisco, barranca de la Guacamaya, Adama, *Mexía 8844* [(♂) F, MO, S, US]. JALISCO: S. of Puerto Vallarta, on canyon slope, *Mexía 1142* [(♂) F, BM, MICH, MO]. MÉXICO: Temascaltepec: Acatitlán, *Hinton 3165* [(♂) US], *3186* [(♀) US], Ixtapan, *Hinton 3643* [(♀) F, MO, US], Pungarancho, *Hinton 6750* [(♀) F, MO, US]. MICHOACÁN: Coalcomán: San Pedro, *Hinton 15901* [(♀) BM, LIL, MICH, US], Aquila, *Hinton 16291* [(♀) US]. NAYARIT: vicinity of Acaponeta, Tepic, *Rose, Standley & Russell 14428* [(♀) US]. OAXACA: Trapiche de la Concepción, *Liebmann 14267* [(♀) C, F, P]; S. Jago Amatlán, *Liebmann 14269* [(♀) C, F]; Between S. Miguel del Puerto & Guatulce, *Liebmann 14271* [(♀) C]; Chinantla, *Liebmann 14270* [(♂) C]. SAN LUIS POTOSÍ: edge of El Salto River, El Naranjo, *Burger 148* [(♀) MO], *150* [(♀) MO]; Tamazunchale, *Edwards 667* [(♀) F]; 7 mi. W. of N. Morelos, Tam., *Kenoyer & Crum 3770* [(♂) MICH]. SINALOA: Cerro Colorado vicinity of Culiacán, *Brandegee S. N.* [(♀ ♂) US]; Mesa Malquesón, Cerro Colorado, *Gentry 5147* [(♀) MICH, MO]; Capadero, Sierra Tacuichamona, *Gentry 5582* [(♀) MO]; Quebrada del Macaral Balboa, San. Ignacio, *Montes & Salazar 855* [(♀) US]; Rosario, Cacalotán, *Ortega 7100* [(♂) F, US]; Marastan, *Ortega 7493* [(♂) US]. SONORA: Quiricoba, Dist. Alamos, *Gentry 736M* [(♀) MICH]. TAMAULIPAS: Tampico de Tamaulipas, *Berlandier 172* [(♀) P]; Rancho Las Yucas, Sa. de Tamaulipas, *Dressler 2372* [(♀) MO]; Julillo to Río Sabinas, N. of Mante, *Duke 3636* [(♀) MO]; near Rancho de Barberena, *LeSueur 570* [(♀) F, US]; vicinity of Tampico, *Palmer* 337 [(♀) F]. VERA CRUZ: *Bonpland 4483* [(♀) P]: Fortín, *Kerber 395* [(♀) BM, C, US]; Mirador, *Liebmann s.n.* [(?) C]; Mirador and Zacuapan, *Liebmann 14268* [C (♀), C (?), F (?)]; Zacuapan, *Liebmann 15111* [(♂) C]; Cordoba, *Matuda 0685* [(♂) MICH, MO, US]; Hda. Mirador, *Nelson 66* [(♀) US]; Is. of Juana Ramírez, 56 km. S. of Tampico, *Palmer 454* [(?) US]; Zacuapan and vicinity, *Purpus 2316* [(♀) F, MO, US], *4386* [(♀) BM, MO, US]. *5049* [(♀) MO, US], *5988* [(♂) BM, F, MO, US], *10837* [(♂) MICH, US], *12072* [(♂) F, MO, US], *14372* [(♂) F]; near Rancho Remudadero, *Purpus 11070* [(♂) F], *11044* [(♂) US], *16381* [(♀) F]; Misantla, *Schiede & Deppe s.n.* [(♀) B, BM, MO]. YUCATÁN: Progreso, *Flores, s.n.* [(♀) F]. WITHOUT PRECISE LOCALITY: Córdova, *Bourgeau 7069* [(♀) P]; *Haenke 1468* [(♂) F]; *Sesse, Mociño, Castillo & Maldonado 4647* [(♂) F].

BRITISH HONDURAS: BELIZE: Bright Lookout Bank, Sibun River, *Gentle 1447* [(♀) F, MICH, MO, US, S]. EL CAYO: Mountain Pine Ridge, *Bartlett 11867* [(?) MICH]; Monkey Falls, *Lundell 6970* [(♂) C, F, MICH, S]. ORANGE WALK: Honey Camp, *Lundell LP19* [(♂) F, US], *Meyer 157* [(?) F]. STANN CREEK: 19 miles, Stann railway, *Gentle 2704* [(♀) F, MICH]; Silk Grass Creek Reserve, *Gentle 3097* [(♀) MICH, MO, US]. TOLEDO: Punta Gorda, *Schipp 1010* [(♂) BM, F, MICH, MO, S]; Big Rock, Toledo, *Schipp 1074* [(♀) BM, F, MICH, MO, S]; Tomash River, *Stevenson 153* [(♀) F]; *Stevenson & Smart 140* [(♂)F, MICH].

GUATEMALA: ALTA VERAPAZ: Saquijá, 43 km. NE. of Cobán, *Standley 70185* [(♂) F]; region of Chelac, NE. of Carchá, *Standley 70403* [(?) F]; Near Pancajché, *Standley 70793* [(?) F]; mountains between Tactic and Cobán, *von Tuerckheim 112167* [(♂) C, US], *112169* [(♀) C, US]; Cubilquitz, *von Tuerckheim 8581* [(♂) F, US]; along river, Chamá, *Johnson 514* [(♂) MO, US]. CHIQUIMULA: Volcán Quezaltepeque *Steyermark 31511* [(♂)

F]. EL PROGRESO: near Finca Piamonto, *Steyermark 43664* [(?) F]. ESCUINTLA: along Río Michatoya, *Standley 89114* [(?) F]. HUEHUETENANGO: between Finca San Rafael and Finca Providencia, *Steyermark 49549* [(♀) F]; along Río Trapichillo, below La Libertad, *Steyermark 51030* [(♂) F]; Paso del Boquerón, along Río Trapichillo, *Steyermark 51185* [(?) F]. IZABAL: near Quiriguá, *Standley 72483* [(♂) F]. PETÉN: Uaxactún, *Bartlett 12354* [(?) F, MICH, US]; Santa Cruz, *Bartlett 12375* [(♀) F, MICH]; Santa Teresa, Subin River, *Lundell 2917* [(♀) BM, F, MICH, S]. RETALHULEU: vicinity of Retalhuleu, Standley *88452* [(?) F], *88549* [(?) F], *88729* [(♂) F]. SANTA ROSA: vicinity of Chiquimulilla, *Standley 79291* [(♀) F]; along Avellana Road, S. of Guazacapán, *Standley 79513* [(♀) F]; *79524* [(?) F]. SUCHITEPÉQUEZ: vicinity of Tiquisate, *Steyermark, 47670* [(?) F], *47774* [(?) F, US]. ZACAPA: Loma El Picacho, *Steyermark 42744* [(♀) F].

EL SALVADOR: CHALATENANGO: *Calderón 2178* [(?) US]. SAN SALVADOR: San Salvador, *Calderón 845* [(♂) US], *1065* [(♂) MO, US], *1448* [(♀) MO, US], *Standley 22458* [(?) US] SAN VICENTE: vicinity of San Vicente, *Standley 21404* [(♀) F, MO, US]. SAN SONSONATE: Izalco, *Calderón 1698* [(?) US]; vicinity of Sonsonate, *Standley 22340* [(?) S, US]. WITHOUT PRECISE LOCALITY: *Renson 112* [(♀) US].

HONDURAS: ATLÁNTIDA: Triunfo, near Tela, *Standley 53841* [(♀) F, US]; Lancetilla Valley, *Standley 54312* [(?) F, US]; vicinity of Tela, *Standley 54727* [(?) F, US]. SANTA BÁRBARA: área de pinoroble de Río Ulúa, *Molina 3810* [(♀) BM, F, MO, US]. TEGUCIGALPA: Mont. de la Flor, *Hagen & Hagen 1130* [(?) F], *1177* [(?) F]. YORO: Concepción, *Edwards P-644* [(♂) F, US]; near Progres, *Standley 54997* [(?) F, US]. WITHOUT PRECISE LOCALITY: Highland Creek, Puerto Sierra, *Wilson 54* [(♀) US], *250* [(♀) US].

NICARAGUA: GRANADA: near Lakes, *Baker 21* [(♂) MICH, MO], *784* [(♂) US]. MANAGUA: between El Crucero and Finca Santa Julia, *Standley 8357* [(?) F]. ZELAYA: vicinity of El Recreo, *Long 215* [(♂) F], *Standley 19797* [(♀) F]; Río Grande, *Molina 2497* [(♀) F, US].

COSTA RICA: PUNTARENAS: Jicaral, *Orozco 406* [(♀) F].

PANAMÁ: BOCAS DEL TORO: Changuinola Valley, region of Almirante, *Cooper 349* [(♀) C, F, US, YU], *Cooper & Slater s.n.* [(♀) F, US, YU], *4* [(♀) US, YU], *4a* [(♀) US, YU], *326* [(♂) F, YU], *Dunlap 16* [(♀) F], *40* [(♀) F]; *Seibert 1581* [(♂) MO, US], *1583* [(?) MO, US]; Chiriquí Lagoon, Water Valley, *von Wedel 1599* [(♀) MO, US]; Old Bank Island, Chiriquí Lagoon, *von Wedel 2075* [(♀) MO, SU]; Río Cricamola, between Finca St. Louis and Konkintoë, *Woodson, Allen & Seibert 1924* [(♀) F, MO]; WITHOUT PRECISE LOCALITY; *von Wedel 196* [(♀) MO]. CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 669* [(♀) F], *Shattuck 827* [(?) F], *1164* [(♀) F], *Standley 41080* [(?) US]; around Culebra, *Pittier 2255* [(♀) US], *3627* [(♀) US]; around Gamboa, *Pittier 6637* [(♂) US], *6652* [(♀) US]; near Gatún, *Standley 27287* [(?) US]; vicinity of Fort Sherman, *Standley 30970* [(?) US]. CHIRIQUÍ: Peninsula de Burica, vicinity of San Bartolomé, *Woodson & Schery 866* [(♀) MO, US]. COLÓN: between France Field C. Z. and Catival, *Standley 30235* [(?) US], *30296* [(?) US]. DARIÉN: between Payo and Palo de las Letras, *Stern et al.* 210 [(?) MO]. PANAMÁ: Taboga, *Hayes 658* [(♂) BM]; Hydrographic Sta., Trinidad River, *Pittier 6636* [(♂) C, P, US]. WITHOUT PRECISE LOCALITY: Western Panama, *Stork 16* [(♀) US].

1c. TROPHIS RACEMOSA SSP. RACEMOSA

Leaf blades elliptic to oblong or ovate, (6.0-) 8.0-18.5 cm. long, 3.0-8.5 cm. wide, acuminate, the acumen usually short and gradually tapering from a broad base, obtuse or occasionally acute at the base, chartaceous to pergamentaceous, smooth on both surfaces, glabrous, the margin entire or occasionally with several deep sinuses. Staminate inflorescences: 3.7-7.5 cm. long, the staminate flowers numerous and densely crowded. Pistillate inflorescences: 0.9-3.8 cm. long, the rachis 1.0-1.8 mm. in diameter, the flowers usually distant along the rachis.

The absence of this subspecies in the Lesser Antilles and its resemblance to ssp. *ramon* suggest that the West Indian plants originally migrated from Central America. Ssp. *racemosa* is quite uniform in its pattern of variation and I have been unable to detect any insular differentiation.

Hillsides and forests from sea level to 1000 meters altitude; flowering from September through March.

Vernacular names: *Ramón* (Cuba, Haiti, and Jamaica); *Ramoon* (Jamaica-Harris); *Ramón de bestia* (Cuba-Ekman).

CUBA: CAMAGUEY: La Gloria to Columbia, *Shafer 617* [(♀) F]. HABANA: near Villa Real, *Ekman 532* [(?) S]. LAS VILLAS: Soledad, Cienfuegos, *Jack 5002* [(♀) P, S], 5842 [(♂) S]. ORIENTE: Bayate, *Ekman 2981* [(♂) S]. *4540* [(?) S], *4594* [(♀) S], 7665 [(♂) S], 9005 [(♂) F, S, (?) S]; Baracoa, *Ekman 4200* [(?) S]; Sierra de Nipe, at Río Piloto, *Ekman 6687* [(♀) S]; La Ermita, *Hioram 4931* [(♂) C]; vicinity of Piedra Gorda, *Shafer 3272* [(♀) F]. Without precise locality, *Wright 589* [BM (♂), S (♀ ♂], *589 & 592* [MO (♀), S (♀ ♂)] *592* [(♀) F, MO, S], *s.n.* [(♀) MO]. PINAR DEL RÍO: Morillo, woods bordering the Manglares, *Ekman 17430* [(?) S]; Las Martinas to the coast, *Shafer 11078* [(♀) F, MO]. WITHOUT PRECISE LOCALITY: *Sagra 490* [(♀) P].

HAITI: OUEST: Massif du Nord, Marmelade, *Ekman 8285* [(♀) S]; Massif de la Selle, Papette, *Ekman 9387* [(♂) S].

JAMAICA: CORNWALL: Trelawny: vicinity of Troy, *Perkins 1005* [(♀) B]; vicinity of Burnt Hill, Cockpit Country, *Proctor 20588* [(♀) BM]. Westmoreland: Kentucky Hill, *Harris 10211* [(♂) BM, F]. MIDDLESEX: Clarendon: Tom's Cave Wood, *Harris 10858* [(♀) F]. SURREY: Portland, John Crow Mts., SW. of Ecclesdown, *Howard, Proctor & Stearn 14782* [(♀) BM]. WITHOUT PRECISE LOCALITY: Cedarhurst, *Harris 6075* [(♀) BM, C]; Hall's Delight, *Harris 5550* [(♀) BM, F].

PUERTO RICO: ARECIBO: Utuado, *Buysman s.n.* (1877) [(♀) MICH], *Sintenis 6309* [(♀) BM, C, F, MO, S]. SAN JUAN: Candelaria, near Bayamón, *Britton, Hess & Marble 2853* [(♀) F, MO]; prope Naranjito, *Stahl 862* [(♀) S].

REPUBLICA DOMINICANA: BARAHONA: *Fuertes 1086* [(♂) BM, F. S]. SAN PEDRO DE MACORIS: *Rose, Fitch & Russell 3719* [(♀) F]; Consuelo, *Taylor 146* [(♀) F], *229* [(♂) F]. WITHOUT PRECISE LOCALITY: *Poiteau, s.n.* (ca. 1882) [(♀) P]; prope Puerto Plata, *Eggers 1769* [(♂) S].

WEST INDIES: WITHOUT PRECISE LOCALITY: *Swartz s.n.* [(♂) S].

2. TROPHIS MEXICANA (Liebm.) Bur. in DC. Prodr. 17:253. 1873.

Sorocea mexicana Liebm. in Kon. Danske Vidensk. Selsk. Skr. 5. 2: 335. 1851. [T.: *Liebmann 14260* (♀) (C)].

Bucephalon mexicanum (Liebm.) O. Ktze. Rev. Gen. 2: 624. 1891.

Trophis chorizantha Standl. in Field Mus. Pub. Bot. 4: 302. 1929. [T.: *Standley 56771* (F) (♀)].

Skutchia caudata Pax & Hoffm. in Journ. Wash. Acad. Sci. 27: 307. 1937. [T.: *Skutch 2383* (US) (♀)].

Trophis matudai Lundell, in Lloydia 2: 81. 1939. [T.: *Matuda 2091* (MICH) (♀)].

Shrubs or trees to 20 m. tall; leafy branchlets slender, 1.5-2.6(-3.2) mm. in diameter, glabrescent or infrequently puberulent, the lenticels small and inconspicuous. Leaf blades elliptic to oblong or occasionally obovate, 8-20 cm. long, 2.5-6.5 cm. broad, acuminate, acute to obtuse at the base, firmly membranaceous to chartaceous, smooth on both surfaces, glabrous above and below or rarely sparsely puberulent below, the midvein plane above, prominent below with 4-9 pairs of ascending secondary veins arching upward near the bluntly serrulate or entire margin; petiole 3-15 mm. long, 0.7-1.5 mm. in diameter, glabrescent. Stipules caducous or occasionally persistent, lanceolate, 2.0-3.6 mm. long, minutely puberulent, their scars small and inconspicuous. Staminate inflorescences: spicate, solitary or less often paired in the axils of leaves or fallen leaves 4-11 cm. long and about 1 cm. in diameter at anthesis, the peduncle 3-12 mm. long, minutely puberulent, the rachis with scattered triangular or suborbicular, basally attached or rarely peltate bracts 0.4-0.8 mm. broad; flowers white or greenish, 13 to many and some-

what distant though appearing crowded at anthesis, sessile or rarely subsessile, about 4 mm. long and 4 mm. wide, the perianth parts 1.5-2.6 mm. long, 0.5-1.3 mm. wide, acute at the apex, connate (0.5-1.3 mm.) toward the base, minutely puberulent, the trichomes less than 0.1 mm. long; staminal filaments 2.0-3.2 mm long, the anthers 0.6-1.2 mm. long; pistillode prominent about 0.6 mm. long. Pistillate inflorescences: racemose, solitary or occasionally paired in the axils of leaves or fallen leaves, (2-)4-10 cm. long, the peduncles 4-25 mm. long, densely puberulent, the rachis with scattered triangular or suborbicular, basally attached or rarely peltate bracts 0.5-1.1 mm. broad; flowers (4-)6-22 and distant, the pedicels (0-)0.5-2.3 mm. long and elongating in fruit, the perianth tube minutely 4-lobed at the apex, ovoid, 1.8-5.0 mm. long, 1.2-2.8 mm. in diameter, sparsely puberulent, the ovary half-inferior, with style branches 2.8-4.5 mm. long and minutely puberulent. Fruit globose, about 5-7 mm. in diameter, strongly ridged or ridged and tuberculate, sparsely puberulent to glabrescent, becoming red, the fruiting pedicels 2.0-6.0(-13) mm. long or the fruit occasionally subsessile.

Plants of Chiapas with subsessile fruit and broad glabrescent leaves have been segregated as *T. matudai*. These specimens resemble *T. racemosa* and are the basis for my impression that *T. mexicana* represents a first divergence from *T. racemosa*. If this is true, *T. mexicana* probably represents the ancestral stock from which closely related *T. chiapensis* and *T. cuspidata* were derived.

Central Mexico to Costa Rica, in moist forests and along water courses; flowering from October to March, from sea level to 2000 m. elevation.

Vernacular names: Sweet breadnut, *Masico dulce* (British Honduras-Gentle); *Ramón blanca* (British Honduras-Lundell); *Raspa-lengua* (El Salvador-Standley).

Mexico: chiapas: Mt. Ovando, Escuintla, *Matuda 0433* [(♂) MICH, US], *0576* [(♀) MICH, NY, US], *2091* [(♀) A, F, MICH, NY, US], *2648* [(♀) A, MICH, NY], *3978* [(♂) F, MICH, MO, NY], *3979* [(♀) A, MICH, NY], *4014* [(♂) A, MICH, MO, NY], *16157* [(♂) F, MICH]. jalisco: La Quadrilla to San Sebastián, *Mexía 1701* [(♂) BM, F, MICH, US]. oaxaca: Cafetal Nueva Esperanza, Pochutla, *Conzatti, Reko & Makrinius 3064* [(♀) US]; Cafetal Concordia, *Morton & Makrinus 2478* [(♀) A, F, S, US]; Cafetal Calvario, Cerro Espino, *Reko 3519* [US (♂) not (♀)]. vera cruz: Hacienda de Jovo, *Liebmann 14260* [(♀) F, photo C].

British Honduras: el cayo: Valentin, *Lundell 6422* [(♀) F, MICH]. stann creek: Stann Creek valley, *Gentle 3211* [(♂) A, MICH, MO, NY]. toledo: Temash River, *Schipp 1334* [(♀) A, BM, F, GH, MICH, MO, NY, S]. without definite locality: Pueblo Viejo, *Schipp 1261* [(♀) A, BM, F, GH, MICH, MO, NY, S].

Guatemala: alta verapaz: between Cobán and San Pedro Carchá, *Standley 89897* [(?) F]; Pansamalá, *von Turckheim 1231* [(♂) F, MO, P, US]. chimaltenango: slopes of Volcán Fuego, *Steyermark 52069* [(?) F]. escuintla: *Aquilar 1645* [(♂) F]; Río Guacalate, *Standley 60197* [(♀) A, F, MICH, NY]; below Las Lajas, *Standley 64766* [(?) F], *64815* [(?) F]; Río Burrión, *Standley 89574* [(?) F]. izabal: Río Juyamá, SE. of Cheyenne, *Steyermark 39157* [(♀) F]; Río Dulce, near Livingston, Steyermark *39451* [(♀) F, NY]. petén: between Finca Yalpemech and Chinajá, *Steyermark 45445* [(♀) F, NY, S]. quezaltenango: Colomba, *Skutch 1986* [(♂) A, BM, F, US]; between Finca Pirineos and Patzulín, *Standley 86697* [(?) F]; slopes of Volcán Santa María, *Steyermark 33499* [(♀) F]. san marcos: slopes of Volcán Tajumulco, *Steyermark 37426* [(♂) F], *37576* [(♂) F]. santa rosa: Cerro Redondo, *Heyde & Lux 6239* [(♂) GH, MO, US]. suchitepéquez: Finca Moca, *Skutch 2094* [(♀) A, BM, F, NY, US].

El Salvador: ahuachápan: Finca Colima, *Standley 20183* [(♀) GH, NY, US].

Honduras: atlántida: near Tela, *Standley 56771* [(♀) F, US]. comayagua: above El Achote, *Yuncker, Dawson, & Youse 6171* [(♀) F, MICH, MO, NY, S, US]. morazán:

Figure 2. *Trophis mexicana:* from *Skutch* 2386 (1), *Skutch 1986* (2), *Schipp 1261* (3), and *Steyermark* 45945 (4).

on and near Mt. Uyuca: *Carlson 2445* [(♀) MICH], *Molina 909* [(♀) F, GH, MO, US], *1108a* [(♀) F, MO, US], *1300* [(♀) F, GH, MO], *1443* [(♀) F, MO], *Pfeifer 1423* [(♀) MO], *Standley 12431* [(♀) F], *20680* [(♀) F], *L. O. Williams 15799* [(♀) F, LIL, MO, US], *16850* [(♀) F, GH, MO, US], *Williams & Molina 14815* [(♀) F, GH] *15601* [(♂) F]. TEGUCIGALPA: San Juancito, *Edwards P-43* [(?) F]. YORO: 10 mi. south of Progreso, *Record & Kuylen H.40* [(♂) GH, NY, US].

NICARAGUA: JINOTEGA: Finca Aventina, *Standley 9965* [(?) F].

COSTA RICA: ALAJUELA: Zarcero, Alfaro Ruiz, *A. Smith H1558* [(♂) F, MO, NY]. GUANACASTE: El Arenal, *Standley & Valerio 45271* [(♂) US]. SAN JOSÉ: vicinity of El General, *Skutch 2383* [(♀) A, MO, NY, S], *2386* [(♂) A, GH, MO, US, S].

3. TROPHIS CHIAPENSIS Brandeg. in Univ. Calif. Pub. Bot. 6: 178. 1915. [T.: *Purpus 7091* (UC) (♀)]

Trophis nubium Standl. in Field Mus. Pub. Bot. 22: 17. 1940. [T.: *Skutch 925* (F) (♀)]

Shrubs or trees to 15 m. tall; leafy branchlets slender 0.8-1.8 (-2.6) mm. in diameter, minutely puberulent and glabrescent, the lenticels small and inconspicuous. Leaf blades narrowly oblong-lanceolate to linear-lanceolate or narrowly elliptic, 5-16 cm. long, 1.2-3.0(-3.8) cm. broad, gradually tapering to the long-acuminate apex, the acumen 1.0-2.5 mm. wide and 5-23 mm. long, acute at the base and often slightly oblique, membranaceous to chartaceous, smooth on both surfaces, glabrous above and below, midvein plane or slightly impressed above, prominent below, with 5-11 pairs of ascending secondary veins arching upward near the serrulate margin; petiole 3.8-12 mm. long, 0.5-1.3 mm. in diameter, sparsely and minutely puberulent, glabrescent. Stipules persistent or caducous, narrowly deltoid to lanceolate, 1.2-3.3 mm. long, minutely puberulent or glabrescent, their scars small and inconspicuous. Staminate inflorescences: racemose, solitary in the axils of leaves or fallen leaves, 1.8-4.2 cm. long, the peduncle 2.4-9.0 mm. long, the rachis with triangular or suborbicular, basally attached bracts 0.4-0.8 mm. broad; flowers white to lavender, 10-35 and usually distant along the rachis, about 5 mm. long and 4 mm. wide, pedicels 0.4-2.8 mm. long, the perianth parts 2.0-2.8 mm. long, the lobes 0.8-1.4 mm. wide, connate by about 25-50% (0.5-1.3 mm.) of their length, minutely puberulent, the trichomes about 0.1 mm. long; staminal filaments 2.0-3.2 mm. long, the anthers 0.8-1.2 mm. long; pistillode prominent, 0.6-0.8 mm. long. Pistillate inflorescences: racemose, solitary in the axils of leaves or fallen leaves, 9-32 mm. long, elongating in fruit, the peduncles 2-7-11.0 mm. long, minutely puberulent, the rachis with numerous triangular or suborbicular, basally attached bracts; flowers 3-14 and distant along the rachis, pedicels (0.3-)0.8-3.0 mm. long, elongating in fruit, the perianth tube 4-lobed at the apex, narrowly ovoid, 1.2-2.6 mm. long, 0.8-1.5 mm. in diameter, sparsely appressed-puberulent, the vesture greenish becoming cinereous; ovary superior to half-inferior, the style branches 2.0-4.2 mm. long. Fruit globose, about 6-8 mm. in diameter, conspicuously tuberculate, glabrate, the fruiting pedicels 3-14 mm. long.

The consistent correlation of narrow leaves and short racemose inflorescences distinguishes this species which ranges from central Mexico to Guatemala.

Central Mexico to Guatemala, in moist forests at altitudes from 800 to 2600 meters; flowering from May to June and October to December.

Figure 3. *Trophis chiapensis*: from *Matuda* 3933 (1: 1.2x), *Skutch 1511* (2), and *Matuda 4241* (3).

Vernacular name: *Cereza de montaña* (Guatemala-Steyermark).

Mexico: chiapas: Mt. Ovando, *Matuda* 3933 [(♀) A, MICH, MO, US]; near Escuintla, *Matuda 4241* [(♂) A, F, MO, US], *15989* [(♂) F, MICH]; Cerro del Boquerón, *Purpus 7091* [(♀) F, MO, US]. guerrero: Montes de Oca, *Hinton 10298* [(♂) GH, US]. vera cruz: Orizaba, *Botteri 1014* [(♂) BM, GH, P]; Palo Dulce, *Mell 685* [(♂) F, NY, US]; Jalapa, *Schiede & Deppe s.n.* [(?) BM, (♂) F]. without precise locality: Sierra San Pedro Nolasco, Talea, *Jurgensen 941* [(♂) BM]; *Mohr 465* [(♂) US].

Guatemala: quezaltenango: Volcán Zunil, *Skutch 925* [(♀) F, MICH, NY, US]; near Santa María de Jesús, *Standley 84572* [(♀) F, S]; between Finca Pirineos and Patzulín, *Standley 86808* [(?) F], *86994* [(?) F], *87012* [(♀) F]; Volcán Santa María, *Steyermark* 33636 [(?) F]. san marcos: Volcán Atitlán, *Skutch 1511* [(♀) A, BM, F, NY, US]: near Rodeo, *Standley 68956* [(?) F]. sololá: Volcán Atitlán, *Steyermark 47833* [(?) F], *47349* [(♂) F], *47392* [(?) F, US]. suchitepéquez: Volcán Santa Clara, *Steyermark 46630* [(♀) F], *46658* [(?) F], *46687* [(♂) F, S], *46730* [(♀) F].

4. Trophis cuspidata Lundell, in Amer. Midl. Nat. 19: 427. 1938. [T.: *Matuda 1051* (MICH) (♂)]

Shrubs or trees to 12 m. tall, the trunk to 30 cm. in diameter; leafy branchlets usually stout, 1.8-4.0 mm. in diameter, puberulent and glabrescent, prominently lenticellate. Leaf blades oblong to elliptic-oblong or elliptic, 10-25 cm. long, 3.0-7.7 cm. broad, narrowly caudate-acuminate, the acumen 1.2-3.0 mm. wide and 1.4-2.8 cm. long, acute to obtuse at the base, firmly membranaceous to chartaceous, smooth and glabrous above, short pilose beneath, the midvein slightly impressed above, prominent below with 7-13 pairs of ascending secondary veins arching upward near the entire margin; petiole 10-24 mm. long, 1.0-2.2 mm. in diameter, densely puberulent. Stipules persistent or caducous, lanceolate, 2.5-3.8 mm. long, their scars often conspicuous. Staminate inflorescences: solitary in the leaf axils, 2-4 cm. long (immature), the perianth parts densely hirtellous. Pistillate inflorescences: racemose, solitary in the axils of leaves or fallen leaves, 2.8-8.0(-12)cm. long, elongating in fruit, the peduncles 7-22 mm. long, densely puberulent, the trichomes about 0.2 mm. long, the rachis with scattered triangular or suborbicular, basally attached bracts 0.5-0.9 mm. broad; flowers 12-30 and distant, pedicels 0.8-3.0 mm. long, elongating in fruit, the perianth tube minutely 4-lobed at the apex, ellipsoid to obovoid, 2.0-4.5 mm. long, 1.5-2.6 mm. in diameter, densely appressed-puberulent, ferruginous or becoming so; ovary half-inferior to inferior, the style branches 2.0-3.7 mm. long, densely and minutely puberulent. Mature fruit not seen.

Characterized by a dense tomentum on floral and vegetative parts and a nearly inferior ovary, this species is closely related to *T. mexicana*.

Southern Mexico and probably extending into Guatemala, at altiudes from 2000 to 4000(?) meters; flowering in December.

Mexico: chiapas: Mt. Ovando, *Matuda 1051* [(♂) MICH, MO]; Mt. Tacaná, *Matuda 2370* [(♀) A, F. MICH, NY]; Pinabeto, Motozintla, *Matuda 15478* [(♀) F].

Excluded Species

Trophis aurantiaca Herzog, in Fedde, Rep. Nov. Spec. 7: 51. 1909.= *Olmedia sp.*

Trophis Hilariana Cazar. Nov. Strip. Bras. Dec. 80. 1845.=*Sorocea guilleminiana* Gaud.

Trophis macrostachya Donn. Sm. in Bot. Gaz. 40: 10. 1905=*Sorocea pubivena* Hemsl.

All the Old World species proposed for *Trophis* are excluded following Bureau in DC. Prodromus 17:254. 1873.

Figure 4. *Trophis cuspidata*: from *Matuda 2370* (1), *Matuda 15478* (2), and *Matuda 1051* (3).

II. CLARISIA R. & P.

Clarisia R. & P. Fl. Per. 128. *t* 28. 1794, nom. conserv., *Clarisia* Abat. [T.: *C. racemosa* R. & P.]

Sahagunia Liebm. in Kon. Danske Vidensk. Selsk. Skr. 5. 2: 316. 1851. [T.: *S. mexicana* Liebm.]

Soaresia, Fr. Allem. in Rev. Brazil. 1: 210: 1857, non *Soaresia* Sch. Bip. [T.: *S. nitida* Fr. Allem.]

Dioecious, laticiferous, unarmed shrubs and trees. Leaves alternate, distichous, bistipulate, pinnately veined, the petioles sulcate above. Stipules lateral, caducous or rarely persistent, their scars encircling less than half the stem. Inflorescences axillary or cauliflorous on the older branchlets; staminate inflorescences spicate with bracts and stamens usually lacking along a narrow line along one or two sides, paired in the axils of leaves or fallen leaves or borne in alternate pairs along a leafless racemiform shoot. Staminate flowers reduced to single stamens arising directly from the rachis, interspersed among numerous bracts, the stamens in well ordered rows or paired but usually irregularly placed, with filaments short and slender, anthers subbasifixed, dehiscing longitudinally. Pistillate flowers pedicellate, with 3-7 suborbicular peltate bracts at the base of the receptacle; perianth tubular, adnate to the inferior ovary; pistil 2-carpellate and 1-locular, the ovule solitary, anatropous and pendulous, the style deeply and narrowly bifid with the stigmatic surface minutely papillate. Fruit drupaceous, the perianth tube accrescent and succulent, the stone ellipsoid, without endosperm, the embryo large with thick equal cotyledons and minute hypocotyl.

Clarisia was revised by Lanjouw in 1936 and many recent collections have been identified according to his revision. The accumulation of new collections with the frequent misplacement of specimens of *Trophis* and *Sorocea* made necessary an examination of material filed under *Clarisia*. In studying this material I have come to conclusions differing from those of Lanjouw though fully cognizant of the contribution his study has made. Lanjouw clarified the nomenclatural problems associated with the name *Clarisia*, which led to the conservation of the genus of Ruiz and Pavón. The major differences between my conclusions and those of Lanjouw are, first, that I have separated the species with capitate pistillate inflorescences as a distinct genus (*Acanthinophyllum*), and secondly, that I interpret *C. biflora* as a polymorphic species of wide distribution. The genus defined in this manner is composed of but two species.

Clarisia presents an interesting sequence in the development of a racemiform inflorescence. The basic condition is probably best illustrated by the pistillate flowers of *C. biflora*. These are usually paired in the axils of leaves but in some specimens they arise in alternating pairs along a shoot that terminates in one to several leaves. In occasional specimens of *C. biflora* the flowering shoots with alternating pairs of flowers are completely leafless [*Allen 3741*, *Weberbauer 7057* (GH)]. The cauliflorous "racemes" of *C. racemosa* with alternating pairs of pistillate flowers or staminate spikes may thus be interpreted as leafless flowering shoots.

The genus extends from central Mexico to Bolivia and eastern Brazil. The trees often reach 30 meters in height and perhaps for this reason are infrequently collected.

KEY TO THE SPECIES

a. Inflorescences axillary on the leafy branchlets; pistillate flowers in axillary pairs or on short leafless racemiform shoots; leaves with 6-12 pairs of ascending secondary veins. Mexico to Bolivia and the upper Amazon basin .....1. C. BIFLORA

aa. Inflorescences cauliflorous on the older branchlets; pistillate flowers on long leafless racemiform shoots; leaves with 10-18 pairs of subhorizontal secondary veins. Ecuador to Bolivia and eastern Brazil .....2. C. RACEMOSA

1. CLARISIA BIFLORA R. & P. Syst. Veg. Fl. Peruv. et Chil. 255. 1798. [T.: *Ruiz & Pavón s.n.* in Herb Madrid]

Shrubs or trees to 35 m. tall, the trunk to 1.2 m. in diameter with smooth brown bark, yellowish wood, and milky latex; leafy branchlets 2.0-4.5 mm. in diameter, sparsely appressed-puberulent, the lenticels small and inconspicuous. Leaf blades narrowly oblong, elliptic-oblong or broadly elliptic, 8-25 cm. long, 2.5-9.0 cm. broad, acuminate, acute to obtuse at the base, firmly membranaceous to stiffly chartaceous, glabrous above, glabrous or sparsely puberulent beneath, the midvein slightly impressed above, prominent below with (4-)6-12 pairs of ascending secondary veins arching upward near the entire margin; petiole (4-)6-22 mm. long, 1.0-2.2 mm. in diameter, minutely and sparsely puberulent, glabrescent. Stipules caducous or rarely persisting, narrowly to broadly cuneate, 3.5-7.2 mm. long, their scars inconspicuous. Staminate inflorescences: spicate, paired in the axils of leaves or fallen leaves or in alternate pairs on leafless racemiform shoots, the primary peduncle 5-35 mm. long, minutely puberulent and bracteate only below the attachment of the secondary peduncles (peduncles of the spikes); spikes 2-10 cm. long, secondary peduncles 3-6 mm. long, sparsely puberulent, the rachis with numerous spatulate to broadly cuneate, basifixed or occasionally peltate bracts; stamens interspersed among the bracts, the filaments straight or sometimes bent below the anther, about 1.0 mm. long, anthers 0.4-0.8 mm. long, emarginate in Mexico, slightly apiculate in Central America, or the connective forming a small apical disc in South America. Pistillate flowers in pairs in the axils of leaves or fallen leaves or occasionally in alternate pairs along a leafless racemiform shoot, peduncles to 12 mm. long, the pedicels 0.5-6.0 mm. long, densely and minutely puberulent, with 3-7 peltate bracts 0.6-1.4 mm. broad at the base of the receptacle; perianth tube 2.2-5.0 mm. long, 1.1-5.0 mm. in diameter, narrowly ovoid to globose, glabrous except at the minutely 2-4 or irregularly lobed apex, style branches 2-6 mm. long. Fruit ovoid to ellipsoid, to 25 mm. long, green or yellowship, smooth and glabrous

This species was interpreted as a group of four by Lanjouw in his revision of 1936. I believe that the additional material now available requires a broader circumscription. The leaves are quite variable and isolated collections have given the impression that this variation is correlated with geography. However, plants with narrow elliptic leaves have now been collected in Costa Rica, Colombia, Peru, Bolivia, and Brazil while broadly elliptic leaves were collected by Ruiz and Pavón in Peru and recently in Panama. The variation in inflorescences likewise is not worthy of taxonomic recognition. The same collection, for example, may have solitary or paired staminate spikes in the axils of leaves [*Skutch 2004* (US)] or leafless racemiform shoots of alternating pairs of spikes [*Skutch 2004* (F)].

The anthers of the only staminate collection from Central American (*Skutch 2004*) possess a slight apical enation that is lacking in specimens from Mexico. I suspect that further collections from Central America will exhibit a transition to the definite disc-like structure of South American specimens. This character of the anthers together with differences in leaf form justifies, I believe, the recognition of two subspecies. The geographical demarcation of these subspecies, however, can only be provisional due to the lack of staminate collections between Guatemala and Colombia.

Key to the Subspecies

a. Anthers emarginate or with the connective only slightly expanded at the apex of the thecae; pistillate flowers globose at anthesis; pedicels 0.5-3.0 mm. long; leaves narrowly oblong to elliptic-oblong. Mexico and Guatemala .....1a. ssp. MEXICANA

aa. Anthers with a definite disc at their apex; pistillate flowers narrowly ovoid to globose at anthesis, pedicels 1-6 mm. long; leaves broadly elliptic to obovate or elliptic oblong. Costa Rica to Brazil and Bolivia .....1b. ssp. BIFLORA

1a. Clarisia biflora ssp. **mexicana** (Liebm.) W. Burger, comb. & stat. nov.

Sahagunia mexicana Liebm. in Kon. Danske Vidensk. Selsk. 5²: 316. [T.: *Liebmann 14259* (C) (♂)]

Clarisia mexicana (Liebm.) Lanj. in Rec. Trav. Bot. Néerl. 33: 270. 1936.

Leaves narrowly oblong to elliptic-oblong or occasionally narrowly obovate, 8-22 cm. long, 2.5-4.5(-7.0) cm. broad, acuminate, acute to obtuse at the base, the secondary veins similar to the lower leaf surface in pigmentation. Staminate spikes to 4.5 cm. long, the anthers eglandular or with a small projection at the apex. Pistillate pedicels 0.5-3.0 mm. long, the flowers globose at anthesis. Fruit not seen.

Flowering from December through March.

Mexico: chiapas: Escuintla, *Matuda 4023* [(♂) MICH, MO], *17439* [(♀) F]. vera cruz: Barranca de Tlatetla, E. of Mirador, *Liebmann 14259* [(♂) F]; Consoquitla. *Liebmann 14273* [(♂) F]; Zacuapan, *Purpus 5989* [(♀) US], *6492* [(♂) F, US].

Guatemala: quezaltenango: Colomba, *Skutch 2003* [(♀) BM, F, US], *2004* [(♂) BM, F, US].

1b. Clarisia biflora ssp. biflora

Sahagunia colombiana Rusby, Descr. New Sp. S. Am. Pl. 10. 1920. [T.: *H. H. Smith 424* (NY) (♂)].

Clarisia colombiana (Rusby) Lanj. in Rec. Trav. Bot. Néerl. 33: 266. 1936.

Clarisia mattogrossensis Lanj. loc. cit. 268. 1936. [T.: *Collenette 131* (K) (♂)].

Clarisia panamensis Woods. in Ann. Missouri Bot. Gard. 47: 123. 1960. [T.: *Allen 3741* (MO) (♀)].

Leaves broadly elliptic to obovate or elliptic-oblong, 7-24 cm. long, 3.2-8.5 cm. broad, often abruptly acuminate, obtuse or occasionally acute at the base, the secondary veins often darkly pigmented. Staminate spikes to 8.5 cm. long, the anthers with a conspicuous gland-like disc at their apex. Pistillate pedicels 1-6 mm. long, the flowers narrowly ovoid to globose at anthesis. Fruit ellipsoid to narrowly oblate, becoming yellowish, with thickened style branches.

The differences in stamen size used by Lanjouw to distinguish *C. colombiana* from *C. mattogrossensis* appear to be due to individual variation and stage of development.

Flowering from December to February and June through September at altitudes to 2100 meters.

Figure 5. *Clarisia biflora.* ssp. *mexicana*: from *Liebmann 14259* (1). ssp. *biflora* from *H. H. Smith 424* (2), *Klug 3698* (3), and *Weberbauer 7057* (4).

Vernacular names: *Lechero colorado* (Colombia-Garcia-Barriga); *Leche caspi, Cuchara caspi* (Peru-Ll. Williams).

Costa Rica: puntarenas: Palmar Norte de Osa, *Allen 5955* [(♀) F, US].
Panamá: coclé; N. of El Valle de Antón, *Allen 3741* [(♀) BM, F, G, MO].
Colombia: cundinamarca: between San Francisco and Subachoque, *Garcia-Barriga 11030* [(♂) US]. santa marta: Don Amo Road, *H. H. Smith 424* [(♂) F, NY, US]. valle del cauca: Cordillera Occidental, Río Sanguinini, *Cuatrecasas 15487* [(♀) F], *15493* [(♂) F].
Peru: libertad: Pataz, below Ongón, *Weberbauer, 7057* [(♀) F, GH]. loreto: Caballococha, Amazon River, *Ll William 2086* [(♀) F]. san martín: Zepelacio, near Moyobama, *Klug 3698* [(♂) BM, F, GH, MO, NY, S]. Lamas, near Tarapoto, *Ll. Williams 6471* [(♂) F]. santa rosa: Urubamba Valley, *Cook & Gilbert 1719* [(♂) F, US]. without precise locality: *Ruiz & Pavón 24 26* [(♀) F], *24/28* [(♀) F]. from Río Ucayli, cult. in Hort. Belém, Pará, Brazil.
Bolivia: la paz: S Yungas, San Bartolomé, *Krukoff 10410* [(♀) F, LIL, MO, S], Larecaja, Tuiri, *Krukoff 10728* [(♀) A, F, LIL, MO, S], *10813* [(♂) F, LIL, MO].
Brazil: acre: São Paulo, Lewin *2076/w17* [(?) LIL]. matto grosso: Tombador, on Rio Serragem, *Collenette 131* [(♂) NY]. pará: in Hort. Belém.

2. Clarisia racemosa R. & P. Syst. Veg. F. Peruv. et Chil. 255. 1798 [T.: *Ruiz & Pavón s.n.*, Chinchao et Pozuzo, in Herb Madrid.]

Soaresia nitida Fr. Allem. in Rev. Brazil 1: 210, *cum tab.* 1857; Arch. Palestr. Scient. Rio Jan. 1: 142. 1858. *ex ic.*
Olmedia erythrorhiza Huber, *nom.* ex Ducke in Arch. Jard. Bot. Rio Jan. 3: 40. 1922, *pro syn.*
Clarisia nitida (Fr. Allem.) Macbr. in Field Mus. Pub. Bot. 11: 15. 1931.

Trees to 40 m. tall, the trunks slender with rough brown bark, yellowish wood, and white latex; leafy branchlets 1.5-3.7 mm. in diameter, minutely puberulent, the lenticels small and inconspicuous. Leaf blades narrowly to broadly oblong or ovate, (4-)6-17 cm. long, (2.0-)3.5-7.0 cm. broad, acuminate, the base often rounded, subtruncate to obtuse or occasionally acute, thickly chartaceous to subcoriaceous, often lustrous above, glabrous, the midvein slightly impressed above, prominent below with 10-18 pairs of subhorizontal secondary veins, the margin entire or slightly undulate; petiole 4-16 mm. long, 0.7-1.8 mm. in diameter, sparsely puberulent and glabrescent. Stipules caducous or rarely persistent, broadly cuneate, 1.2-2.0 mm. long, their scars small and inconspicuous. Staminate inflorescences: cauliflorous, solitary or several arising together from the older branchlets, usually of alternate pairs of spikes along a leafless racemiform shoot, 6-15 cm. long, the primary peduncle 5-43 mm. long, minutely puberulent or glabrescent, the primary rachis bracteate only below the attachment of the secondary peduncles (peduncles of the spikes); spikes 2-9 cm. long, secondary peduncles 2-10 mm. long, densely and minutely puberulent, the rachis of the spike with numerous spatulate to broadly cuneate, basifixed or occasionally peltate bracts; stamens interspersed among the bracts, the filaments about 1.0 mm. long, anthers about 0.5 mm. long, emarginate. Pistillate inflorescences: racemiform, cauliflorous on the leafless branchlets or rarely in the axils of leaves, solitary to several arising together, 6-14 cm. long (to 25 cm. in fruit), the 10-24 flowers usually borne in alternate pairs along a leafless racemiform shoot (inflorescence); peduncle 12-35 mm. long, the rachis glabrescent and bracteate only below the attachments of the pedicels; pedicels 2.4-4.5 mm. long (to 20 cm. in fruit), densely and minutely puberulent, occasionally with a bract

Figure 6. *Clarisia racemosa:* from *Ducke (30/VI/1942) 948* (1), *Ducke (26/X/1935) 59* (2), *Krukoff 5380* (3), *Krukoff 10744* (4), and *Krukoff 8312* (5).

or two along their length, with 3-5 suborbicular peltate bracts 0.7-1.5 mm. broad at the base of the receptacle; perianth tube narrowly to broadly ovoid, glabrous but appressed-puberulent at the irregularly lobed apex, 3.5-8.0 mm. long; style branches 5-10 mm. long. Fruit ellipsoid or somewhat asymmetric, to 35 mm. long and 14 mm. in diameter, orange becoming black, smooth and glabrous.

The inflorescences show little of the variation found in *C. biflora* and apparently have become stabilized. An interesting exception is the British Museum specimen of *Krukoff 1450* with two solitary, long-pedicelled pistillate flowers in the axils of leaves. Other specimens of the same collection possess the normal cauliflorous "racemes." The disjunct plants of Rio de Janeiro exhibit no morphological distinctions that might be correlated with their isolation.

Ecuador to Bolivia and eastern Brazil; in moist forests and the *matta de terra firme* and *várzeas* of the Amazon basin. Flowering from July to January.

Vernacular names: *Moral babo, Moral comida de mono, sota, zota* (Ecuador-Little); *Capinuri* (Peru-Ll. Williams); *Tulpay* (Peru-Burgos); *Guariuba* (Peru and Brazil-Ll. Williams, Ducke, Krukoff, et al.).

Ecuador: esmeraldas: near Quininde, *Little 6219* [(?) F].

Peru: huánuco: Km. 142 Huánuco-Pucallpa, *Burgos 59* [(?) F]. junín: La Merced, *Weberbauer 1912* [(♀ ♂) F]; Río Negro, *Woytkowski 5865* [(♀) MO]. loreto: R'o Ucayli, *Tessmann 5433* [(♂) S]; La Victoria, *Ll. Williams 2684* [(?) F], *3079* [(?) F]; Alto Río Itaya, *Ll. Wiliams 3380* [(?) F]. without precise locality: *Ruiz & Pavón 24/24* [(?) F].

Bolivia: la paz: S. Yungas, Río Bopi, *Krukoff 10533* [(♂) F, LIL, MO, S], *10679* [(?) F]; Larecaja, Tuiri, *Krukoff 10744* [(?) F, LIL, MO, S].

Brazil: acre: mouth of Rio Macauhan, *Krukoff 5380* [(♀) A, BM, F, MO S]: Rio Acre, Ule 9317 [(♂) MG]. amazonas: Manáus, *Ducke (26/X/1935) 59* [(♂) A, F, MO, RB, S]; basin of Rio Solimões, *Froes 132* [(♀) LIL]; São Gabriel, Rio Negro, *Froes 410* [(?) LIL], 852 [(?) LIL]; mouth of Rio Embira, *Krukoff 5173* [(♀) BM, F, MO, S]; Humayatá, near Tres Casas, *Krukoff 6327* [(♀) BM, LIL, MO, S]; near Livramento, *Krukoff 6628* [(♀) A, BM, F, MO, S]; São Paulo de Olivença, *Krukoff 8312* [(♀) BM, F, MICH, MO, RB, S], *8666* [(♀) BM, F, MICH, P, S]. matto grosso: near Tabajara, *Krukoff 1450* [(♀) A, BM, MO, S]. pará: Tapajos, Bôa Vista, *Capucho 568* [(♀) F]; Faro, *Ducke (2/I/1920) 13051* [(♀) RB, S]; Gurupá, *Ducke (14/VIII/1918)* [(?) MG]; Rio Rapajoz, São Luiz, *Ducke (4/XII/1919) 13052* [(♀) P, RB, S], *(14/XII/1919) 13052* [(♂) S]; Rio Trombetas, *Ducke (18/II/1918) 16993* [(?) MG], *(25/X/1919) 13054* [(♂) RB, SS]; Rio Xingú, *Ducke (14/X/1916) 16606* [(♂) MG, P, RB]. rio de janeiro: Corcovado, *Glaziou 20489* [B (♀ ♂), C (♀ ♂), P (♂)]; Cosmo Velho, *Glaziou 8289* [(♀) F, P]; Rio de Janeiro, *Kuhlmann (VIII/1920) 13055* [RB (♀ ♂), S (♂)], *(19/IX/1920) 13055* [(♀) S].

Excluded Species

Clarisia ilicifolia (Spreng.)—Lanj. & Rossb. in Rec. Trav. Bot. Néerl. 33:717. 1936. =*Acanthinophyllum ilicifolia* (Spreng.) W. Burger.

Clarisia mollis Standl. in Ann. Missouri Bot. Gard. 30:85. 1943. =*Sorocea pubivena* Hemsl.

Clarisia spruceana Lanj. in Rec. Trav. Bot. Néerl. 33:272. 1936. =*Acanthinophyllum spruceana* (Lanj.) W. Burger.

Clarisia strepitans (Fr. Allem.) Lanj. in Rec. Trav. Bot. Néerl. 33:272. 1936. =*Acanthinophyllum ilicifolia* (Spreng.) W. Burger.

Clarisia urophylla (Donn. Sm.) Lanj. loc. cit. 270. 1936. =*Trophis racemosa* (L.) Urb.

III. ACANTHINOPHYLLUM Fr. Allem

ACANTHINOPHYLLUM Fr. Allem. in Rev. Brazil. 1:368, 1858; Arch. Palestr. Scient. Rio Jan. 1:215. 1858. [T.: *A. strepitans* Fr. Allem., =*A. ilicifolia* (Spreng.) W. Burger]

Dioecious, laticiferous, unarmed shrubs and small trees. Leaves alternate, distichous, bistipulate, pinnately veined, the petioles sulcate above. Stipules lateral, caducous or persistent, their scars encircling less than half the stem. Inflorescences axillary or cauliflorous on the leafless branchlets, solitary or several clustered on leafless brachyblasts or rarely the staminate alternate along a short leafless racemiform shoot, the staminate spicate with the bracts and stamens lacking along a narrow strip along one side, the pistillate capitate; peduncles densely invested with minute retrorse uncinate trichomes. Staminate flowers reduced to single stamens arising directly from the rachis and interspersed among numerous variously shaped bracts, occasionally in groups of 2-4; filaments short and slender, the anthers small and usually dorsifixed, dehiscing longitudinally. Pistillate flowers sessile on a short peduncled capitulum; perianth tubular, free or partially adnate to the superior or subinferior ovary; pistil 2-carpellate, 1-locular, the ovule solitary, pendulous, and anatropous, the style shortly bifid with the inner stigmatic surface glabrous. Fruit drupaceous, the perianth tube accrescent and succulent, the stone globose to ellipsoid, without endosperm, the embryo large, straight, and erect with thick, usually equal cotyledons, the hypocotyl minute.

The genus ranges from British Guiana to eastern Brazil and the Amazon basin of Venezuela, Brazil, and Bolivia.

Acanthinophyllum is characterized by its staminate flowers reduced to single stamens and its pistillate flowers borne on a short peduncled capitulum. Liebmann described *Sahagunia* from staminate plants he had collected in Mexico. When Bentham and Hooker (1880) described the pistillate flowers of the genus *Sahagunia* they unfortunately drew their details from specimens of *Acanthinophyllum*, which is restricted to South America. The staminate spikes of *Acanthinophyllum* resemble those of *Sahagunia* but the dorsifixed anthers and pistillate capitula readily distinguish the two genera. The retrorse uncinate trichomes present on leaves, twigs, and especially peduncles of *Acanthinophyllum* are not found in *Clarisia* (an earlier name for *Sahagunia*). In addition to the trichomes the midvein of the leaves is prominulous above and the epidermal cells have a deeply sinuate outline. These vegetative characters are shared, to my knowledge, only by *Trymatococcus* and *Helianthostylis* among South American Moraceae. The genus is represented by two species.

KEY TO THE SPECIES

a. Staminate spikes condensed, to 2.0 cm. long; pistillate inflorenscences of 8-15 closely contiguous flowers; leaves spinulose-serrate to entire. British Guiana to Brazil and Bolivia ..... 1. A. ILICIFOLIA

aa. Staminate spikes lax, to 6.5 cm. long; pistillate flowers not seen; leaves entire. Venezuela: Amazonas ..... 2. A. SPRUCEANA

1. ACANTHINOPHYLLUM **ilicifolia** (Spreng.) W. Burger, comb. nov.

Excoecaria ilicifolia Spreng. Neue Entdeck. 2: 117. 1821. [T.: *Without Collector*, "in **Brasilia," in Herb. Berlin, (♂)**]

Acanthinophyllum strepitans Fr. Allem. in Rev. Brazil. 1: 36, *cum tab.* 1858; and in Arch. da Palestr. Scient. Rio Jan. 1: 215. 1858. *ex ic.*

Pseudosorocea Poeppigii Baill. in Adansonia 11: 297. 1875.

Sahagunia strepitans (Fr. Allem.) Benth. & Hook. Gen. Pl. 3: 377. 1889.

Sahagunia racemifera Huber, in Bol. Mus. Para. 5: 334. 1908. [T.: *Ducke (27/VII/1902)* 2885 (MG) (♂)]

Sorocea stenophylla Standl. in Trop. Woods no. 43: 18. 1935. [T.: *Capucho 447* (F) (♀)]

Clarisia strepitans (Fr. Allem.) Lanj. in Rec. Trav. Bot. Néerl. 33: 274. 1936.

Clarisia strepitans var. *guianensis* Lanj. loc. cit. 274. 1936. [T.: *Stahel 120* (U) [(♀)]

Clarisia strepitans var. *paraensis* Lanj. loc. cit. 275. 1936. [T.: *Huber 6965* (U) (♀)]

Clarisia strepitans var. *micranthera* Lanj. loc. cit. 275. 1936. [T.: *Glaziou 12172* (K) (♂)]

Clarisia strepitans var. *cuyunensis* Lanj. loc. cit. 275. 1936. [T.: *Forest Dept. 1029* (U) (♂)]

Clarisia ilicifolia (Spreng.) Lanj. & Rossb. loc. cit. 717. 1936.

Clarisia ilicifolia var. *guianensis* (Lanj.) Lanj. & Rossb. loc. cit. 718. 1936.

Clarisia ilicifolia var. *paraensis* (Lanj.) Lanj. & Rossb. loc. cit. 1936.

Clarisia ilicifolia var. *micranthera* (Lanj.) Lanj. & Rossb. loc. cit. 718. 1936.

Clarisia ilicifolia var. *cuyunensis* (Lanj.) Lanj. & Rossb. loc. cit. 718. 1936.

Shrubs or small trees to 8(-15) m. tall with white or yellowish latex; leafy branchlets sparsely invested with small retrorse uncinate trichomes, glabrescent, the lenticels small and inconspicuous. Leaf blades elliptic to elliptic-oblong, obovate or occasionally linear-lanceolate, 3-25 cm. long, 1.7-7.0(-9.0) cm. broad, acuminate to abruptly caudate-acuminate, the apex acute, acute to obtuse at the base, chartaceous to pergamentaceous, glabrous, the midvein prominulous above, prominent below with 6-14 pairs of ascending secondary veins arching upward near the spinulose-serrate to entire or occasionally deeply sinuate margin; petiole 5-17 mm. long, 0.7-2.5 mm. in diameter, glabrescent or sparsely invested with retrorse uncinate trichomes. Stipules caducous or persistent narrowly lanceolate, 1.0-1.8 mm. long their scars small and inconspicuous. Staminate inflorescences: spicate, axillary or cauliflorous on the older branchlets, paired, solitary, or clustered on leafless brachyblasts or rarely on leafless racemiform shoots, 4-20 mm. long; peduncles 2-5 mm. long, densely invested with small retrorse uncinate trichomes, the rachis with numerous cuneate to suborbicular, basally attached or occasionally peltate bracts; stamens interspersed among the bracts, the filaments about 1 mm. long, the anthers 0.2-0.3 mm. long, occasionally paired or rarely in threes. Pistillate inflorescences: capitula of 8-15 closely contiguous flowers, solitary, paired or clustered on leafless brachyblasts in axils of leaves or cauliflorous, 10-18 mm. long at anthesis; peduncles 3-9 mm. long, densely invested with retrorse uncinate trichomes about 0.1 mm. long; flowers occasionally subtended by basally attached bracts, elliptic to obovoid or variously shaped by contact with adjacent flowers, sessile, the perianth tube 1.2-3.0 mm. long, 1.0-3.0 mm. in diameter, minutely hispidulous, the ovary superior to subinferior, tapering to the slender style, style branches broad, about 1-2 mm. long, glabrous. Fruit globose or ellipsoid, to 25 mm. long and 15 mm. in diameter, smooth and glabrous, orange at maturity.

The leaves of this species are extremely variable, ranging from broadly elliptic to linear-lanceolate and from spinulose-serrate to entire. This variability is found

Figure 7. *Acanthinophyllum ilicifolia*: from *Ducke* (2/IX 1923) 18326 (1 & 2: stamen X20), *Krukoff* 1669 (3), *Krukoff* 5991 (4), and *Capucho* 447 (5 & 6).

throughout the range of the species except for the very narrow-leaved specimens which have only been collected in Pará. Standley's *Sorocea stenophylla* (Plate 7, fig. 5) is based on a collection with linear-lanceolate leaves and may be worthy of varietal status. Collections from Amazonas have more ellipsoid fruit and fewer spinulose leaves than specimens from Pará, but these characters are too inconstant to establish subspecies and I am not describing categories below that rank. Lanjouw described four varieties of which var. *guianensis* with large broadly elliptic leaves appears to be most distinct; however I have not seen var. *cuyunensis*.

Flowering from June to December in moist forest and the *mata de terra firme* of the Amazon basin.

Vernacular names: *Bainha de espada* (Rio de Janeiro-Allemão); *Folha de serra* (Minas Gerais-Magalhães); *Janita* (Pará-Ducke).

French Guiana: Karoumany, *Sagot 530* [BM (?), P (♂), (?)]; Without precise locality, *Poiteau s.n.* 1844 [(♂) B].

Bolivia: Río Serra, *Kuhlmann 571* [(♀) RB].

Brazil: acre: Rio Abunan, *Kuhlmann (21/X/1923 675* [(?) RB]. amazonas: Calama, Madeira River, *Krukoff 1309* [(♀) BM, MO, NY, P, S]; Borba, near Bella Vista, *Krukoff 5991* [(?) S]; Manicoré, near Santa Fé, *Krukoff 6049* [(♀) BM, F, LIL, MO, NY, S]; Humayatá, near Livramento, *Krukoff 6849* [(♀) A, BM, F, MO, P, S]; Democracia, Madeira River, *Kuhlmann (31/VIII/1923) 257* [(♂) RB, S], *(31/VIII/1923) 284* [(♀) RB]; Maués, *Pires 118* [(♀) NY); Santarém, *Ginzburger et al. 854* [(♀) F]. guaporé: Jatuarana River source, *Krukoff 1669* [(♀) BM, MO, P, S]. maranhão: *Maracassumé*, Bôa Esperança, *Froes 1869* [(♂) BM, F, MO, P, S], *Moses 65* [(?) BM]. matto grosso: Ouro Preto, *Kuhlmann (20/IX/1923) 487* [(♀) RB]. minas gerais: Campo de Cementes, *Magalhães 843* [(♀) US]; Barbado, *Mexia 5158* [(♂) A, BM, F, GH, MICH, MO, NY]; Lagôa Santa, *Warming s.n.* [(?) S]. pará: Belterra, *Black 47-1715* [(♀) NY], *47-1728* [(?) NY]; Tapajos, Bôa Vista, *Capucho 447* [(♀) F]; Obidos, *Ducke (29/VII/1902) 2885* [(♂) MG, RB]. *(23/XII/1907) 9190* [(♀) MG, RB], *(28/XII/1913) 15270* [(♀) BM, MG, RB], *(13/IX/1926) 19473* [(♂) RB, S]; Alemquer, *Ducke (26/XII/1903) 4899* [(♂) BM, MG, RB]; Rio Cuminá, *Ducke (13/X/1913) 14978* [(♂) BM, MG, RB]; Monte Alegre, *Ducke (24/IV/1916) 16059* [(♂) MG]; Bragança, *Ducke (10/II/1923) 18323* [(♀) RB]; Rio Tapajoz, *(22/VIII/1923) 18324* [(♂) RB, S]; Serra de Santarém, *Ducke (2/IX/1923) 18325* [(♂) RB], *18326* [(♂) RB, S]; Belém, Bosque Municipal, *Ducke (10/VII/1945) 1726* [(♂) A, F, MG]; Manáus, *Francisco-INPA 2025* [(♂) MG]; Moema, *Herb. Amaz. 9572* [(?) MG, RB]; Belém do Pará, Santa Izabal, *Huber 6894* [(♀) MG, RB]; without definite locality. *Huber 6965* [(♀) S]; Trav. Barão d'Mamoré, *Signiera 3657* [(♂) MG, RB]; Ourém, *Signeira 4022* [(♂) BM, RB]. rio de janeiro: matas do Horto Florestal, *Duarte & Pereira 01574* [(♀) RB]; Corcovado, *Ducke & Kuhlmann 6153* [(?) RB]; Trapicheira, *Ducke & Kuhlmann 19697* [(?) RB], *Kuhlmann 1906* [(?) RB], *19292* [(♀) RB]; entre Mendanha et Realengo, *Glaziou 12172* [(♂) B, C, F, P]; S. José, *Peckholt s.n.* Nov '86 [(♀) B]. without precise locality: *Glaziou 1470* [(?) C]; Castelnovo, *Riedel s.n.* Sept. 1822 [(?) US]; *Sello s.n. 1815-1817* (♂) BM].

2. Acanthinophyllum **spruceana** (Lanj.) W. Burger, comb. nov.

Clarisia Spruceana Lanj. in Rec. Trav. Bot. Néerl. 33: 272. 1936. [T.: *Spruce 3279* (K) (♂)]

Small trees with slender glabrescent branchlets, the lenticels small and inconspicuous. Leaf blades oblong to elliptic-oblong, 8-17(-21) cm. long, 3.2-6.7 cm. broad, acuminate, acute to slightly rounded at the base, chartaceous to pergamentaceous, glabrous, the midvein prominulous above, prominent below with 7-13 pairs of ascending secondary veins arching upward near the entire margin to form an arcuate marginal vein; petiole 8-12 mm. long, 1.2-1.7 mm. in diameter, glabrescent

and rugose. Stipules caducous, their scars small and inconspicuous. Staminate inflorescences: spicate, 2-4 clustered leafless brachyblasts, 2.0-6.5 cm. long; penducle 4-10 mm. long, densely invested with retrorse uncinate trichomes, the rachis with numerous cuneate to suborbicular, basally attached or subpeltate bracts; stamens interspersed among the bracts or in groups of 2-4, the filaments about 1 mm. long, somewhat flattened, anthers 0.2-0.3 mm. long. Pistillate flowers not seen.

A. spruceana is quite distinct though represented solely by Spruce's original collection. The isotype in the British Museum does not possess the rounded leaf base of the original description.

VENEZUELA: AMAZONAS: ad flumina Casiquieri, Vasiva et Pacimoni, *Spruce 3279* [(♂) BM].

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ENUMERATION OF THE GENERA AND SPECIES

I. TROPHIS
- 1. *racemosa* (L.) Urb.
  - 1a. ssp. **meridionalis** (Bur.) W. Burger
  - 1b. ssp. **ramon** (Schlecht. & Cham.) W. Burger
  - 1c. ssp. *racemosa*
- 2. *mexicana* (Liebm.) Bur.
- 3. *chiapensis* Brandeg.
- 4. *cuspidata* Lundell

II. CLARISIA
- 1. *biflora* R. & P.
  - 1a. ssp. **mexicana** (Liebm.) W. Burger
  - 1b. ssp. *biflora*
- 2. *racemosa* R. & P.

III. ACANTHINOPHYLLUM
- 1. **ilicifolia** (Spreng.) W. Burger
- 2. **spruceana** (Lanj.) W. Burger

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Cha cox ..... I 1b
Cuchara caspi ..... II 1b
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Moral babo ..... II 2
Moral comida de mono ..... II 2
Ojoche macho ..... I 1b
Ojushte ..... I 1b
Ramón ..... I 1b
Ramón blanca ..... I 2
Ramón colorado ..... I 1b
Ramón de bestia ..... I 1b
Ramoon ..... I 1b
Raspa-lengua ..... I 2

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Ujushte	I 1b	*Zota*	II 2

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Italicized numerals refer to collectors' numbers, *s.n.* (*sine numero*) to unnumbered collections; parenthetical numerals refer to the numerals of taxa conserved in this revision: the Roman to genera, and the Arabic to species; lower case letters refer to subspecies.

Allen, P. H. *3741, 5955* (II 1b).
Aquilar, J. *1645* (I 2).
Asplund, E. *9387* (I 1a).
Bailey, L. H. & E. Z. Bailey *669* (I 1b).
Baker, C. F. *21, 784* (I 1b)
Bartlett, H. H. *11867, 12354, 12375* (I 1b)
Berlandier, J. L. *172* (I 1b).
Black, G. A. *47-1715, 47-1728* (III 1).
Bonpland, A. *1512* (I 1a); *4485* (I 1b).
Botteri, M. *1014* (I 3).
Bourgeau, M. *7069* (I 1b).
Brandegee, T. S. *s.n.* (I 1b).
Britton, N. L., W. E. Hess & D. W. Marble 2853 (I 1c).
Burger, W. C. *148, 150* (I 1b).
Burgos, J. A. *59* (II 2).
Buysmann, M. *s.n.* (I 1c).
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POLLINATION AND VARIATION IN THE SUBTRIBE CATASETINAE (ORCHIDACEAE)

CALAWAY H. DODSON

ABSTRACT

The natural history of the subtribe Catasetinae is briefly discussed. The present taxonomic status of the genera *Catasetum, Cycnoches* and *Mormodes* is reviewed, and the phylogenic relationships between the genera and the species groups in *Catasetum* are discussed. The production of separate male and female inflorescences is explained as being triggered by the relative amounts of sunlight received by the plants. Those plants which receive filtered sunlight produce male flowers and those receiving full sunlight produce female flowers. The pollen throwing apparatus and the pollination mechanisms of the various genera are discussed on the basis of field observations. Variation in populations of *Catasetum platyglossum* Schltr. and *C. macroglossum* Rehb. f., which are sympatric on one margin of their ranges in western Ecuador, is evaluated. The two populations were once separated by a band of rainforest on a low mountain range. This region has become sufficiently arid for the species to come together and pollination by a common agent has produced several highly variable hybrid swarms. CALAWAY H. DODSON, Missouri Botantical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

INTRODUCTION

This paper has been written to discuss in a general manner, the pollination, pollination mechanisms, taxonomy, relationships among the members, sexuality and population variation of the Catasetinae. It is hoped that in this manner a basic reference will be formed for forthcoming papers dealing with specific phenomena in the group. The present status of taxonomy in the group is deplorably bad and classic herbarium techniques of study are of little or no help in critical groups, due to the general paucity of specimens and the destruction of important characters in their preparation. Field studies of population variation will surely be important in clarifying the taxonomy of the group.

The subtribe Catasetinae has been of interest to both botanists and horticulturists since the members of this group became known. The complicated mechanisms enabling forcible discharge of the pollen apparatus found in most species have been described and commented upon by various authors. Such highly evolved mechanisms capture the interest of anyone from the orchid enthusiast to the evolutionist and considerable literature is available on the mechanics of these systems. However, very few accurate observations have been made upon the natural pollination of these plants in the field. Authoritative accounts have been published of pollination in *Cycnoches* by Allen (1952) and in *Catasetum* by Darwin (1872), based on observations by Crüger. Unfortunately, Crüger's account was based on very superficial observation and both papers contain some errors and omit considerable pertinent information.

This group is unique among the Orchidaceae for having members which produce separate staminate and pistillate flowers. They are also unique in having the capacity of forcibly flinging the pollinarium at an insect pollinator. The pollinarium is thereby fixed in such a position on the insect that it may easily complete the pollination phase of the life cycle by delivering the pollen to the stigma of another flower.

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* Much of the work done for this paper was supported by a grant from the National Science Foundation (G-19957).

Taxonomy of the Group

As presently constituted the subtribe Catasetinae consists of three genera, *Catasetum* Rich. with approximately 70 nominal species, *Mormodes* Lindl. with about 40 nominal species and *Cycnoches* Lindl. with seven species. The group is limited to the New World tropics where its members occasionally form a conspicuous element in the orchid flora. Its closest affinities probably lie with *Cyrtopodium* R. Br. and *Galeandra* Lindl. of the subtribe Cyrtopodiinae. While the linking members between these genera and the Catasetinae are now extinct, the gap is not great.

Catasetum has been divided into two subgenera; *Clowesia* and *Catasetum*. The subgenus *Clowesia*, as treated by Mansfeld (1932) and Hoehne (1942), consisted of eight species all of which produce bisexual flowers and have no antennae on the column to trigger the expulsion of the pollinaria. Two quite dissimilar groups have been placed together in *Clowesia* and it is my opinion that they should eventually be separated. *Castasetum roseum* Rchb. f., *C. warczewitzii* Lindl. & Paxt., *C. glaucoglossum* Rchb. f. *C. thylaciochilum* Lem. and *C. russellianum* Hook., have the lip relatively thin in substance, not adnate to the column and usually fimbriate. In *C. glaucoglossum* and *C. russellianum* the anther is only slightly sensitive and the viscidium springs down only slightly when released. These species have many characters in common with certain species of *Galeandra*. The other group consists of *C. dilectum* Rchb. f., *C. eburneum* Rolfe and *C. suave* Ames and Schweinfurth. Unfortunately, there appear to be only two species in this group, but there are three names; two of which are of uncertain application. One species, corresponding to *C. suave* of Ames and Schweinfurth (the type of this species, at the Smithsonian Institution, has been examined) occurs from Costa Rica to Ecuador. The other species is only to be found in Costa Rica and Panama. Both species are somewhat variable and the type descriptions are not satisfactory to differentiate between the two kinds of plants. These species have the lip entire, fleshy and adnate to the thick, swollen column. I feel that this group is adequately distinct from the other group of species in Clowesia and should be recognized as a valid genus.

The subgenus *Catasetum* as treated by Mansfeld and Hoehne consists of nearly 60 species, all producing separate male and female flowers. The subgenera *Clowesia* and *Catasetum* are not far separated in terms of evolution and the development of unisexual flowers from the bisexual group is easily traced. The column of most species of the subgenus *Catasetum* has long projections or antennae extending from each side of the anther to the center or cavity of the lip. These antennae, when touched, release the tightly stretched stipe of the pollinarium so that the viscidium is flung out and onto the thorax of the insect. Mansfeld divided the subgenus *Catasetum* into two groups; *Pseudocatasetum* and *Meizocatasetum*, the former having male flowers which are devoid of antennae and the latter having antennae. He then went further to divide *Meizocatasetum* into two groups; *Isoceras* and *Anisoceras*, depending on whether the antennae were parallel or one was bent back under the other. I have found this division to be unworkable on many occasions

in which some flowers had the antennae parallel, while others on the same inflorescence had one bent. In other instances one inflorescence would have flowers with antennae bent and another inflorescence of the same plant would have flowers with parallel antennae. The flower morphology is not particularly distinct between the two subgenera and the more advanced members of *Clowesia* closely approach the species which lack antennae in the subgenus *Catasetum*. Even in the more advanced members of the subgenus *Catasetum* hermaphroditic flowers are occasionally produced which are quite reminiscent of some members of *Clowesia*.

Cycnoches has been revised recently by Allen (1952). Allen's treatment of this genus is unusual in modern taxonomic work on the tropical Orchidaceae in that it is based on personal knowledge of the plants as living populations in the field. *Cycnoches* is composed of two distinct subgenera. In the subgenus *Cycnoches* the male and female flowers are essentially the same in form with the only significant difference being that the column is shorter and thicker with the stigma functional in the female flowers while the column is long and slender with only the anther present in the male flowers. Allen lists four species in this subgenus. The subgenus *Heteranthae* produces male and female flowers which are strikingly different. The female flowers are morphologically similar to the female flowers of the subgenus *Cycnoches* but are smaller. The male flowers are much smaller than the female flowers, are produced in considerable quantity on long pendant racemes, have a flexible claw on the lip and usually have a toothed fleshy callus. Allen lists three species in this subgenus.

Mormodes has never been revised. This is probably due to the formidable variation encountered within the populations. In several cases, characters which were previously used to separate species have been found to vary widely on one inflorescence. Certainly many of the 40 nominal species will be found not to be valid when a careful study is made of the genus.

Phylogenetic Relationships Within the Catasetinae

The ancestral types linking the subtribe Catasetinae with its closest allies in the Cyrtopodiinae are now extinct but sufficent correlation between the two subtribes remains to indicate relationship.

A phyletic series can be observed from *Catasetum glaucoglossum* and *C. thylaciochilum* as the simplest types through *C. russellianum* to *C. roseum* and *C. warczewitzii* in the subgenus *Clowesia*. The sensitive anther which is characteristic of the Catasetinae is not highly developed in some of the members of this group. *Catasetum discolor* of the subgenus *Catasetum* is morphologically quite similar to *C. warczewitzii* except that separate male and female flowers are produced. More advanced species are then encountered with unisexual flowers and are furnished with complicated antennae for triggering pollinia expulsion. In the latter group the species with rather similar hooded male and female flowers are probably less advanced than the species with open male flowers (such as *C. barbatum* Lindl.) which have highly developed fringes and papillae on the lip of the male flower.

The basic separation between the types of flowers produced by the major groups

of *Catasetum* is morphological but is founded upon different pollination mechanisms. In the portion of the subgenus *Clowesia* which produce less fleshy flowers the column is of necessity placed relatively near the lip in order for the pollinator to brush the anther with its upper thorax and receive the pollinarium. *Catasetum roseum, C. thylaciochilum, C. warczewitzii, C. russellianum* and *C. glaucoglossum* all appear to be of this type. *Catasetum dilectum, C. eburneum* and *C. suave* appear to be based on another system in which the bee approaches the flower, lands on the front of the open flower with its head toward the apex of the lip and its abdomen over the column, touches the triggering mechanism and receives the pollinia on the ventral side of the thorax either in front of or among the legs. In the more advanced species of *Catasetum* the bee lands upon the lip and while approaching the source of the fragrance, located in a depression or within a saccate hood, inadvertantly touches one of the antennae, releasing the pollinarium which is flung for some distance to strike the pollinator. The pollinator is usually positioned in such a manner that the viscidium is attached to the upper thorax.

Cycnoches may have developed from the fleshy flowered group of species in the subgenus *Clowesia* of *Catasetum*. Though the general features of the labellum are not entirely similar in the two groups, the apparatus for expulsion of the pollinarium is very similar. Both types of flowers are designed for placement of the pollinarium on the ventral surface of the pollinator. In *Catasetum suave*, for example, the column is short and fleshy with the anther positioned on the apex of the column. The simple extension of the anther on a long, slender column would result in the same type of apparatus as found in *Cycnoches*. The triggering mechanisms for expulsion of the pollinia in the two groups are based upon leverage and tension released by lifting the apex of the anther. These two groups are the only members of the Catasetinae which use this system for propulsion of the pollinia (fig. 1). The fleshy members of *Clowesia* are normally quite uncommon in nature, perhaps an indication that they are not particularly successful. They are only found in the tropical cloud forest regions of Central and South America. These cloud forests seem to be particularly hospitable for relict and marginal epiphytic species.

Cycnoches has apparently left the bisexual flowered condition and normally only exhibits unisexual flowers. The occasional production of hermaphroditic flowers indicates that the capacity for production of bisexual flowers is not completely lost.

The genus *Mormodes* is apparently in the process of developing unisexual flowers at present. There have been reports of the production of unisexual flowers in certain species of *Mormodes* and I have encountered the same condition in a species in Ecuador. This genus is perhaps not as highly successful as *Catasetum* or *Cycnoches*. Within their range they are usually not encountered in such great quantity as the other two genera and are often quite rare. The plants are not as tolerant of adverse ecological conditions as are the related genera.

Sexuality

The production of unisexual flowers in these orchids has been the subject of considerable comment and discussion. It is, of course, unique in a family nearly typified by bisexual flowers. This development of polygamo-dicecious flowers appears to be in a stage of transition in certain species within the Catasetinae. The species within the subgenus *Clowesia* of *Catasetum* apparently produce bisexual flowers only, while the members of the subgenus *Catasetum* ordinarily produce unisexual flowers. Species of the subgenus *Catasetum* do occasionally produce bisexual flowers, and both male and female flowers are sometimes found on the same inflorescence. Within the genus *Cycnoches* no species occur which produce bisexual flowers exclusively, but bisexual flowers are found on these plants on rare occasions. Recent evidence (Allen 1959) indicates that two types of flowers are found in *Mormodes lineatum* Batem.; staminate flowers, which apparently function only as male flowers, and perfect flowers which produce functional pollinia as well as a functional stigma. The two types of flowers are different morphologically but a transition can be found between them. I have observed the same situation in *M. buccinator* Lindl., from central Ecuador. Certain plants were noted which produced the same large flowered type with little contortion of the column and a very large stigmatic surface which Allen noted in *M. lineatum*. On other occasions the same plants produced smaller flowers with strongly contorted columns and reduced stigmas.

Figure 1. Action of the pollinaria discharging apparatus in the various groups within the Catasetinae. The arrow indicates the point of contact which releases the stipe. a. *Catasetum thylaciochilum* Lem. b. *Catasetum russellianum* Hook. (Slightly exaggerated). c. *Catasetum discolor* Lindl. d. *Catasetum platyglossum* Schltr. e. *Catasetum* aff. *suave* A. & S. f. *Cycnoches ventricosum* Batem. g. *Mormodes buccinator* Lindl.

Figure 2 shows two views of a flower of *M. colossus*, the first taken with the anther in place and the second taken 24 hours after removal of the anther. The column has straightened and reorganized itself so as to function as a female flower. This phenomenon has not yet been observed in other species of *Mormodes*.

Figure 2. Twisting of the colum in *Mormodes colossus* Rchb. f. a. Flower with the anther in place. b. The same flower 24 hours after removal of the pollinarium.

The factors which make it possible for a plant of this group to produce male flowers during one season, female flowers in the following season and perhaps a mixed inflorescence in the succeeding season have never been clearly explained. There has been considerable speculation about temperature relations triggering one type or the other. Also an intrinsic ability on the part of the plant to decide whether it should produce one sex or the other has been suggested. Studies made by the author over a 14 month period in coastal Ecuador involving *Catasetum macroglossum* Rchb. f., *C. platyglossum* Schltr., *Cycnoches lehmannii* Rchb. f., and *Mormodes buccinator* Lindl., indicate that the production of male versus female flowers depends primarily upon ecological factors. When a plant growing in full sunlight has adequate moisture during the growing season and has its roots embedded in a suitable substrate (rotting wood is apparently most favorable) it will be robust and will generally produce female flowers. If on the other hand, either sunlight or humidity is lacking, or the plant is growing on the bark of relatively smooth-barked tree, it will normally not be as robust and will produce male flowers. The substrate does not appear to be as important as the other two factors for plants with female inflorescences have occasionally been observed on living trees, though in all such cases the trees had deeply fissured bark. The factor of sunlight appears to be particularly important.

Experiments conducted at the Instutito Botánico of the University of Guayaquil indicated that the sex of the flower could be changed during one season. Thirty robust plants of *Catasetum macroglossum* with female flowers which had been in full sunlight under natural conditions were brought in and 15 were placed in dense shade and 15 in full sun. These plants had produced their first inflorescences before the full development of the pseudobulb and still retained their leaves. New inflorescences were produced and all plants in shade flowered male. Thirteen plants placed in full sun continued to produce female inflorescences. Two plants which were not quite as robust as others produced inflorescences with both male and female flowers present. Large plants which had produced male inflorescences in

the early part of the season produced female inflorescences when placed in full sun for the remainder of the season.

It seems clear from these experiments that determination of sex depends largely upon growing conditions of the individual plant. Robust plants growing in full sun usually produce female inflorescences. The chemical differences in the plants which are producing one sex as opposed to plants producing the other have not been investigated. There is the possibility that the production of female flowers may be due to carbohydrate balance or, on the other hand, it may also be due to a hormone balance which is affected by sunlight. A similar situation has been reported in *Cannabis sativa* in which the production of male or female flowers was controlled by presence or absence of hormones.

As a general rule very few plants in a population are growing under conditions conducive to the production of female flowers. In the *Catasetum macroglossum* populations growing in the tropical deciduous forests of coastal Ecuador, approximately 21 male inflorescences for each female inflorescence were counted. In populations growing in the regions of greater humidity which are now planted to cacao and coffee, the trees provide considerable shade and the count was 46 male inflorescences to one female. In populations of *Cycnoches lehmannii* growing in old cacao plantations around Quevedo the count was 27 male inflorescences to one female. No accurate results were obtained in the population of *Mormodes buccinator* due to the shortage of specimens, however it was noted that the only two plants which produced the female type inflorescences were growing in full sun in ant nests and had extremely large and robust pseudobulbs. Seven other plants were found growing in partial shade which did not have large pseudobulbs and all produced male inflorescences.

The discrepancy in numbers between the male and female inflorescences produced is apparently important in the ecology of the plants. As a rule the male flowers in all species are short lived, lasting at most four or five days. Their segments are usually thin in substance and wilt within hours after the pollinaria have been discharged. Within two or three days after opening their fragrance becomes strong and they wilt shortly thereafter. If the pollinator does not discharge the pollinarium within a day or two after the fragrance becomes strong they are often discharged automatically or by the slightest movement of the wind. The female flowers, on the contrary, are very long lasting, occasionally persisting up to six weeks. They are usually large and of very heavy, fleshy substance and do not emit their fragrance until seven or eight days after they have opened. It would seem logical that more male flowers would be needed since insect visitation is often rather haphazard and it would be highly important to the fertilization of the female flowers to have a large quantity of short-lived, fragrant male flowers in the vicinity. With a succession of numerous short-lived male flowers available to the pollinators the possibilities of the pollinator having pollinaria attached when he visits the female flower would be greater.

Pollination

Pollination within the subtribe Catasetinae is very poorly documented and the accounts which have been published are inaccurate in many points. We have

observed pollination in *Catasetum macroglossum*, *C. platyglossum*, *C. suave*, *Cycnoches lehmannii*, *C. egertonianum* and *Mormodes buccinator* (Dodson & Frymire 1961b). Allen (1952) has reported the pollination of *Cycnoches ventricosum*, *Catasetum oerstedii* and *Mormodes histrio*. Hoehne (1933) reported on *Catasetum cernuum*. Östlund (unpublished) very accurately recorded the pollination of *Mormodes histrio*, *M. uncia* and *M. lineatum*. Unfortunately, these species represent a very small portion of the actual number of species in the subtribe but they do represent both subgenera in *Catasetum* and *Cycnoches*, and four species of *Mormodes*. A discussion of pollination in each of the species which we observed should establish the basic patterns of pollination involved.

It would appear that all species in the Catasetinae are pollinated by bees of the family Apidae, subfamily Euglossini. Two genera important in pollination of the Catasetinae are *Eulaema* and *Euglossa*. We have not observed any other visitors to the flowers. For a more extensive discussion of these bees and their habits see Dodson (1962).

Pollination of *Catasetum suave* (this name is tentatively used until the identity of earlier names can be definitely fixed) was observed in June of 1960 at a site 12 kilometers east of Balzapamba on the road to Guaranda in the Province of Bolívar. This locality is on the western slope of the Andes at an elevation of 1400 meters. The plants are terrestrial and grow on the faces of road cuts. Pollination is effected by males of *Eulaema cingulata* (L.). The bees approach the flowers, which are carried on racemes of 10-20 flowers each, and land upon the open surface of a flower attempting to reach the source of the strong clove oil-like fragrance which emanates from the cavity of the lip (fig. 3). The flowers are nonresupinate, therefore the lip is uppermost in the flower. In attempting to thrust its head into the cavity of the lip, the bee moves the small hump on the anther cap and the stipe is released, flinging the sticky viscidium upwards where it strikes the bee either on the trochanters of his legs or in front of the first pair of legs. The stipe of the pollinarium, immediately after attachment to the bee, is curled and does not dry and straighten out for several minutes. This tends to insure that the bee will have flown on to another plant and will effect cross-pollination. The viscidium covers the stigmatic surface of the flower so that the pollinarium must be removed before pollination can occur. When a bee with pollinarium attached comes to a flower and repeats the attempt to enter, the pollinia are guided into the stigmatic cavity, trapped in the narrow extremities of the cavity, and pulled from the bee upon his exit from the flower.

Lankester (1960) reports the pollination of the other species from this group, which he (possibly quite correctly) called *C. dilectum*. The flowers of this species are essentially similar to *C. suave*. The primary differences between the two species lie in the sub-capitate inflorescence, strongly reflexed tepals, smaller flowers and enlarged callus of *C. dilectum*. According to Lankester *C. dilectum* is pollinated by a species of Euglossa. His description indicates that the activity of the bees is similar to what I observed in the pollination of *C. suave*.

Figure 3. *Eulaema cingulata* (Fab.) visiting the flowers of *Catasetum* aff. *suave* A. & S.

Catasetum russellianum is representative of the closed flowered types of the subgenus *Clowesia* and experiments with living male bees of *Eulaema cingulata* at the Missouri Botanical Garden indicate that this species of Catasetum with its only slightly sensitive anther uses a different mechanical system for attaching the pollinarium. The bee, in attempting to reach the saccate portion of the lip, near the base of the column, touches the stipe of the pollinarium and the viscidium is released and swings down into such a position that in withdrawing from the flower the bee will push against the viscidium with its metathorax. Upon subsequent entrance and exit from another flower—allowing time for the anther cap to dry and fall—the pollinia are left behind in the narrow stigmatic cavity.

The subgenus *Catasetum* has a rather different system of pollination primarily because there are two sexes of flower involved. Two species from this section were observed and have essentially the same system although the flower form is different. Two or three days after opening, the mature hood shaped male flowers of *C. macroglossum* begin emitting a strong musky odor. Male bees of four species of *Eulaema* were observed visiting the flowers. These were *E. cingulata* (L), *E. tropica* (L), *E. bomboides* Friese and E. *speciosa* Moc. The bees grasp the labellum, which in this species of *Catasetum* is uppermost in the flower, and enter upside down (Fig. 4). After entry they do not extend their tongues, but scratch the inner surface of the labellum with their fore legs using the same action as a dog digging a hole. At the same time their antennae brush over the scratched surface. Chemoreceptive pads on the tarsi of the bees (which are present in all male bees of the Euglossini) apparently allow the bee to taste the liquid which is emitted from the scratched surface of the labellum. While scratching at the inner surface of the saccate

Figure 4. Illustration of the pollination of *Catasetum macroglossum* Rchb. f. by *Eulaema cingulata* (Fab.). a. Male bee entering the male flower. b. The bee scratching at the surface of the lip and touching the antenna which fires the pollinaria out toward the pollinator with the viscidium striking the thorax of the bee. c. Bee in flight with the pollinarium attached to its thorax after the anther cap has fallen. d. Same bee entering the female flower and scratching the surface. e. Bee preparing to leave the flower. Note the pollinia being guided into the stigmatic pocket of the column where they are removed by leverage as the bee struggles free.

labellum the bee contacts one of the antennae which are extensions of the sides of the rostellum and hold the anther cap and stipe of the pollinarium under tension. The tips of the antennae are located just over the deepest point of the saccate labellum where the strongest odor is emitted. The movement of the antennae triggers the release of the pollinarium. The pollinarium is propelled upward and outward, the sticky surface of the viscidium foremost, and is stuck to the thorax of the bee. The adhesive substance of the viscidium sets rapidly, and the stipe hinges back at the point of attachment to the viscidium lying flat along the dorsal mid-line of the abdomen of the bee. The bee may then proceed in its wandering to a mature, aromatic, female flower.

The female flower takes somewhat longer to mature than does the male and begins to give off a strong odor on the third or fourth day after opening. The non-resupinate female flowers last up to a month if not pollinated and continue to emit their strong fragrance during the day; however, the fragrance disappears within hours after pollination, and the stigma swells shut. Bees are attracted to and enter the female flowers much as they do in the male flowers. When a bee with a pollinarium attached to its thorax enters a flower, the stipe, hinging at the viscidium, swings down in line with the stigmatic cleft. As the bee backs out to leave the flower, one or both of the pollen masses are guided down on the back side of the lip and are caught in the stigmatic cleft. They are then wrenched free—by leverage—from the weak bonds with the stipe and are left to fertilize the flower.

Pollination in *C. platyglossum* is essentially identical, the only major difference being that the male flowers are resupinate with the open lip lowermost in the flower (Fig. 5). The bee simply lands on the open labellum, walks to the basal cavity and touches the antennae, setting off the same process as in *C. macroglossum*. The female flowers are so nearly identical to *C. macroglossum* that it is not possible to separate the two species from the female flower alone.

Hoehne (1933) has reported on the pollination of *Catasetum cernuum* (Lindl) Rchb. f., in Brazil, by *Euglossa violacea*. *Catasetum cernuum* is similar in many respects to *C. platyglossum*, having male flowers which are open rather than hooded as in *C. macroglossum* and its allies. The flowers of *C. cernuum* are considerably smaller than those of *C. platyglossum* and are highly colored with orange and red

Figure 5. a. Male *Eulaema tropica* (L.) visiting the male flowers of *Catasetum* aff. *platyglossum* Schltr. b. Male *Eulaema cingulata* (Fab.) visiting the female flowers of *Catasetum platyglossum* Schltr.

spots. This species is representative of a large number of species from South America which have open male flowers and more or less fimbriate lips. Hoehne's description indicates that the pollination process is essentially the same in this species as in *C. platyglossum* with the exception that *C. cernuum* utilizes bees of the genus *Euglossa* as pollinators. Probably most of the species in the group allied to *C. cernuum* are pollinated by Euglossas.

The pollination process in *Cycnoches lehmannii* appears very complex but in reality is quite simple. The system depends on perfect placement of the bee in relation to the lip and sexual apparatus of the flower. In order to place the bee properly the flower has developed a lip which is nonresupinate, forcing the bee to land in an inverted position, with the source of the odor located at the apex of the callus of the lip. The female flowers appear to have an odor that is a little stronger

Figure 6. Male *Eulaema cingulata* (Fab.) pollinating *Cycnoches lehmannii* Lindl. a. The bee has touched the apex of the anther cap with its abdomen causing the pollinarium to be discharged and the viscidium to be attached to the apex of the abdomen. b. Male bee scratching at the apex of the callus of the lip of the female flower. c. Bee falling from the callus of the female flower (note the pollinarium extended from the abdomen of the bee which will be caught by the hooks of the apex of the column).

and more penetrating than the male flowers. The male bee of *Eulaema cingulata* approaches the male flower and lands on the inverted lip, gradually swinging around into an inverted position with the 2nd and 3rd pair of legs grasping the edges of the lip. (Fig 6). The first pair of legs are brushed back and forth on the apex of the callus. The odor appears to emanate from between the apex of the callus and the lip. The extended callus of the male flower forces the bee—in attempting to get closer to the source of the odor—to swing his abdomen down and release his lower pair of legs. This is an extremely awkward position for the bee and the lower portion of the adbomen of the bee brushes the trigger mechanism of the column. The brushing of the tip of the anther cap releases the viscidium which is held under tension in what would normally be the stigmatic region in a bisexual flower. The stipe whips the viscidium around striking the bee on the last sternum of the abdomen where it sticks by means of its rapid drying cement. The anther cap remains over the pollinia and the stipe is curled around the tip of the bee's abdomen. The stipe of the pollinarium, through differential drying of the two surfaces, gradually straightens out and after about 40 minutes has straightened to a stiff pendant position. The anther cap remains in place covering the pollinia for about two to three hours before drying sufficiently to fall off. The pollinarium is then ready for the bee to pollinate the female flower.

The female flower is constructed differently. The position of the column and stigma is quite different from the male flower in relation to the callus, being much shorter and thicker. The callus is not as extended as in the male flower and the bee has little difficulty in hanging and scratching on the callus tip. When the bee is ready to fly he must fall for a short distance to be able to revert to a flying position. In falling, the bee, through his predetermined position on the callus is oriented in such a manner that in passing the column the pollinia are caught by the finger-like processes of that structure. One of the pollinia is caught and is stripped from the stipe. Within a few hours the stigma swells, closing around the pollinia, the odor ceases, and the flower parts wither; the pod ripens about a year after pollination.

Pollination of *Cycnoches egertonianum Batem.* was observed in the Amazon drainage area of the southeast Ecuador. *Cycnoches egertonianum* is a member of the heteromorphic group of *Cycnoches* in which the male flowers—unlike the group to which *C. lehmannii* belongs—are strikingly different from the female flowers. The male flowers of this species are small and are carried on long pendant racemes. The lip is somewhat different from that of *C. lehmannii* in that the claw is thin and flexible and the blade is divided into numerous fleshy terete divisions. Male bees of *Euglossa viridissima* were observed pollinating this species. (Fig. 7). The bees would land on the blade of the lip which would then swing down with the weight of the bee. This action caused the tip of the bee's abdomen to touch and lift the anther cap on the apex of the column, discharging the pollinarium which became affixed to the bee much as in *Cycnoches lehmannii.* The female flowers are nearly identical to those of *C. lehmannii* except that they are somewhat smaller and are darker green in color. The pollination of the female flower is essentially the same as discussed in *C. lehmannii* above.

Pollination of *Mormodes* has been reported for four species (Allen 1952 and Östlund unpublished). We observed bees with pollinia attached to their thorax visiting the female flowers of *M.* aff. *buccinator* in Ecuador. The bees, *Euglossa viridissima*, landed on the outstretched lip and proceeded to scratch the surface of the lip with their front pair of feet. (Fig. 8). In moving around on the lip the pollinaria on their backs came in contact with the very broad stigmatic surface and the pollinia became detached. Though the anther of the pistillate flower in *Mormodes* can eject the pollinarium, it is held up and far away from the lip of the flower in a position which would be very difficult for a bee to encounter and discharge. In the male flowers the column is twisted in such a way that the apex of the column lies in contact with the lip. Usually the twisting places the back of the column in contact with the lip and the anther, located on the ventral surface, is facing outward. A small terete finger or tubercle formed from the tip of the column is in contact with the tip of the anther cap. This tubercle lies on the surface of the lip and the slightest movement moves the anther cap allowing the viscidium to be released. The viscidium, carried by the stipe, springs around and strikes any object which has moved the tubercle. The cement on the viscidium quickly dries leaving the pollinarium attached to the insect. After about 30 minutes have passed the stipe

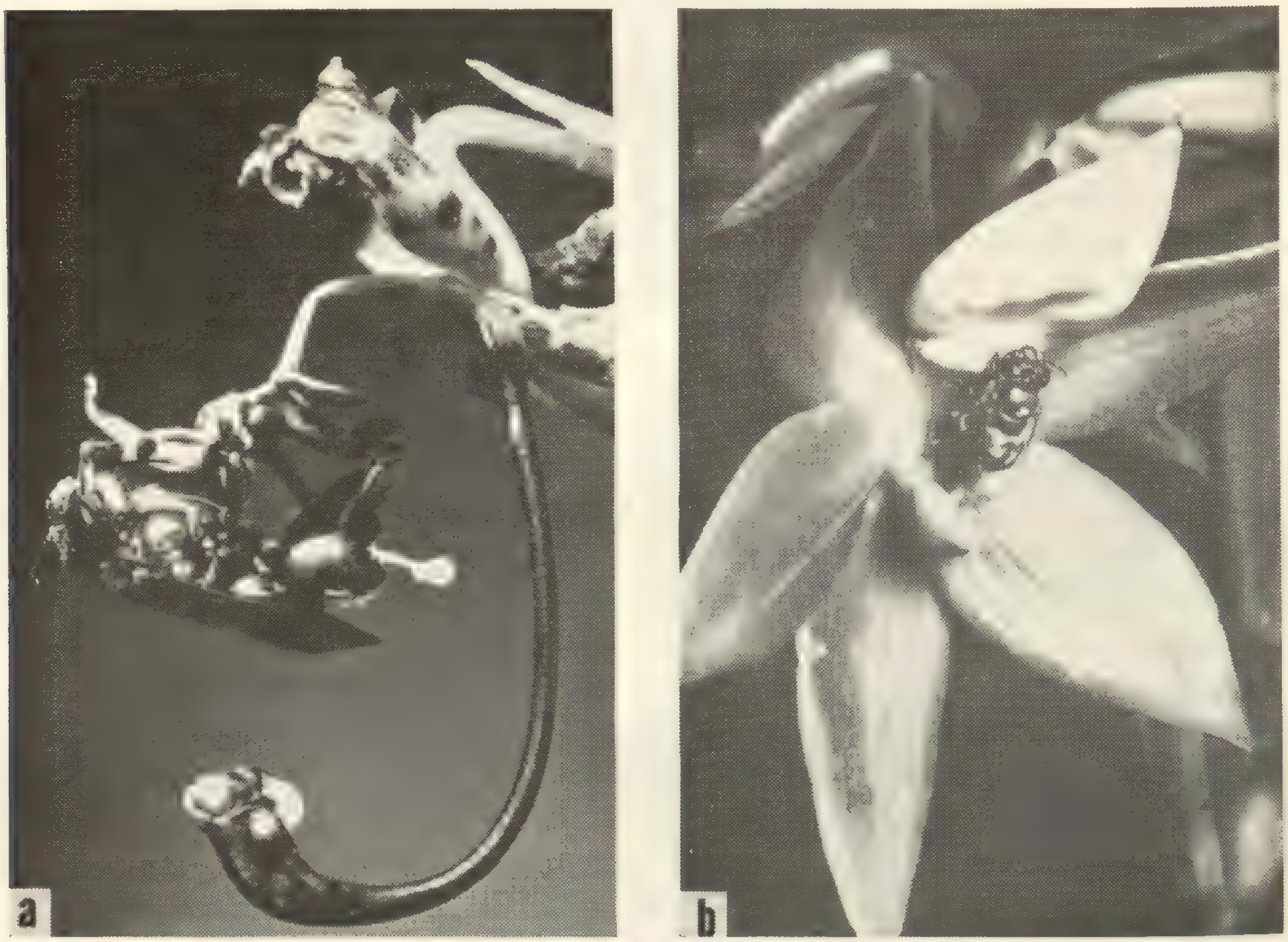

Figure 7. Male *Euglossa viridissima* Fr. pollinating *Cycnoches egertonianum* Batem. a. Male bee hanging from the flexible lip of the male flower (note the pollinarium extending from the apex of the abdomen of the bee). b. Male bee scratching at the callus of the lip of the female flower (note the pollinarium which has been deposited in the stigma).

straightens and the pollinia are held erect from the thorax of the bee in such a position that when the bee walks under the stigma of a flower, contact is made.

Figure 8. Male *Euglossa viridissima* Fr. pollinating the flower of *Mormodes buccinator* Lindl. a. Bee walking around on the lip of the flower immediately after discharging the pollinarium which can be seen curled up and attached to the thorax of the bee. b. The same bee at a later time showing the pollinarium attached to the thorax of the bee. (Note that the stipe of the pollinarium has straightened placing the pollinia in position to be deposited on the stigma in the background.

In no instance of pollination observed by me, in any of the above mentioned species of the Catasetinae, did the bees gnaw on the lips of the flowers as reported by Darwin (1877), Crüger (1865), Porsch (1955), Allen (1952 & 1959) and as so eloquently described by Ames in *Catasetum* (1945). The bees were never noted by us to even touch the surface of the labellum with their mandibles and they did not extend their tongues. It is possible that chewing or gnawing do actually occur during pollination of these orchid species in Panama or Trinidad but this hardly seems reasonable since the same species of bees are involved as in Ecuador. Östlund (unpublished) reports the same phenomen of scratching in the pollination of *Mormodes lineatum* in Mexico. He also pointed out that the bees did not gnaw the flowers.

We have noted numerous small bees and wasps which do gnaw the flowers of these and other orchids but which are too tiny to actually effect pollination. None of the Catasetinae provide nectar or has nectaries. The bees, apparently in all cases, scratch the surface of the lip at the point of origin of the odor and then touch the liquid released, with the sensory pads on their feet. This liquid appears to have an intoxicating effect on the bees because they cease to be wary and then can be approached without being frightened. The bees often spend considerable time at one plant and will enter the same flower repeatedly. On each occasion, they enter, scratch the surface of the lip for about 60 seconds, leave the flower and hover for about 40-60 seconds, apparently checking for danger, and then reenter the flower. After the bees have been visiting a particular flower for some time, it can even be removed and the bee will continue to search out that flower from the odor.

Perhaps the most significant factor brought out by these observations is the fact that in both *Catasetum* and *Cycnoches*, species groups have become both morphologically and ecologically distinct by their adaptation to different kinds of pollinators. Of even greater interest is the fact that the two kinds of pollinators are

closely related, have similar habits and similar morphology. Their principal differences are in size and response to different fragrances produced by the flowers for their attraction. Indications are that the bees have been on the scene for a much greater period of time than the orchids. The orchids have been able to utilize the two types of bees as a crutch, so to speak, in speciation. The opportunity of using different kinds of pollinators, which would not overlap and thereby would not nullify the adaptation to distinct mechanical systems, may be as important in speciation to a group of this nature as are the development of incompatibility and genetic barriers to crossing in many other groups of flowering plants. Speciation in these orchids could occur by adaptation to one pollinator and later to another and then back again. Such speciation would, of necessity, be on a large scale with drastic changes in morphology of the flowers expected. Elimination of intermediates by early extinction would leave large discontinuity between groups and would present to the systematist clear-cut groups even at the generic level. The development of such strikingly different morphological features as found in the Catasetinae and the Stanhopeinae (Dodson and Frymire 1961a) may be attributable to just this sort of speciation.

Variation in Populations

Population variation in the subtribe Catasetinae has long been a problem in species classification. The problems in this group are not so great on the generic level. For the most part the genera are amply distinct, but the delineation of species has been unusually difficult. Taxonomists working with preserved material have been plagued by this problem and the all too common solution has been to describe each troublesome specimen as a new species, based upon the obvious floral differences from any other known species. Unfortunately, though this has been the easiest method for handling the problem, it has not reflected species differences. Until recently no studies have been attempted on extensive living populations in their natural habitats.

The problem of extreme population variability is not peculiar to the Catasetinae. It is also quite evident in certain species of nearly all genera of the Stanhopeinae, the Maxillariinae and in many genera of the Oncidiinae and Epidendrinae. The only usable taxonomic treatments of large variable groups in the orchids have been done recently by Paul Allen in *Cycnoches* (1952) and *Chysis* (1955). His treatments of these two troublesome genera reflect his deep knowledge of the extent of population variation gained by personal knowledge of the taxa involved. His reduction of a series of 50 named species of Cycnoches to 7 with 4 subspecies demonstrates, for the first time in the group, not only the excessive number of named variants but also phylogenetic trends within the group. As an example, he reduced 14 named species to one, *Cycnoches egertonianum* and retained three subspecies which represent geographical and population trends.

Similar work is needed in the genera *Catasetum* and *Mormodes*. Many names have been applied to individual variants from variable populations of *Catasetum*, particularly in South America where population studies have been nonexistent and few preserved specimens are available in herbaria. In many cases names have been applied to plants without any knowledge of their origin.

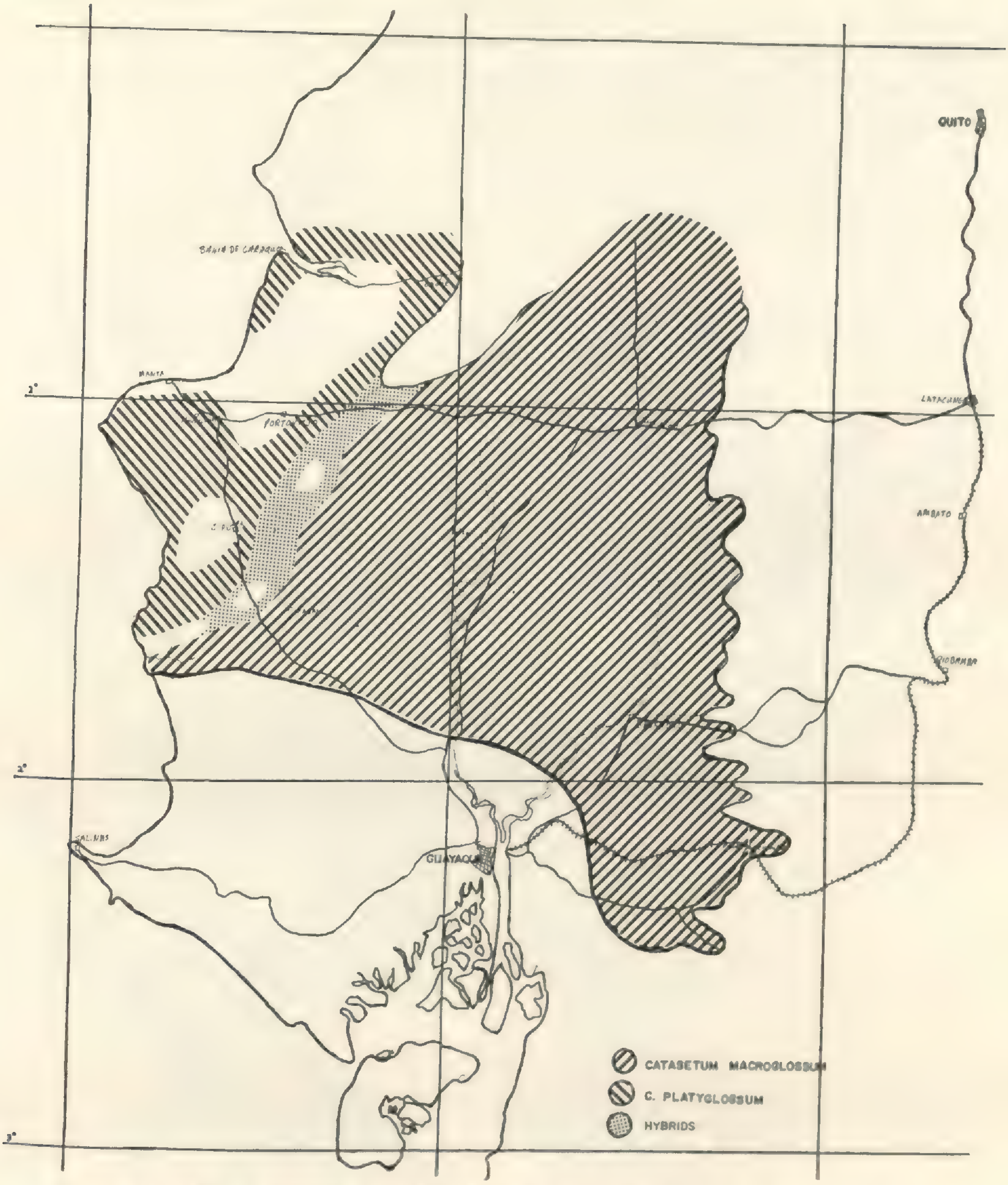

Figure 9. Map of western Ecuador showing the distribution of *Catasetum macroglossum* Rchb. f., *C. platyglossum* Schltr. and their hybrids.

In coastal Ecuador, populations of two highly confused species of *Catasetum* are found in quantity. These are *C. macroglossum* and *C. platyglossum*. During the early months of 1958, 1960, and 1962 I had the opportunity to observe and study hundreds of flowering plants of these species and some rather startling observations were made. The two species were apparently once separated by a range of mountains, the Cerros de Colonche, which run north and south through the coastal plain paralleling the Andes. These mountains effectively split the coastal plain into two valleys with the eastern valley about 50 miles wide and flanked by

the Andes on the eastern side. The western valley is about 30 miles wide and is flanked by the Pacific Ocean. A large rather dense and variable population of *Catasetum macroglossum* occupies the eastern valley and *C. platyglossum* occurs in a sparse population in the western valley (see Fig. 9).

Figure 10. *Catasetum macroglossum* Rchb. f. showing two inflorescences, the female to the left and the male to the right.

Figure 11. *Catasetum platyglossum* Schltr. showing the male inflorescence.

Until recently [probably less than 200 years as established by comparison of the grazing areas of livestock during the colonial period (1600-1700) and the map in Wolf's *Geografía y Geología del Ecuador* (1892)] the Cerros de Colonche with its rainforest-clad slopes provided an effective barrier to gene exchange. A drying trend throughout the coast, caused by an apparent shift in the Humboldt current, has reduced the width of the rainforest, particularly in the passes between the higher areas. In these passes the two species have come together and the result has been the production of a series of hybrid swarms of bewildering variation.

Figure 10 shows a plant with male and female inflorescences of what could be considered as typical *C. macroglossum*. Figure 11 represents a plant with a male inflorescence of typical *C. platyglossum*. The female flowers of both are so nearly identical that no statistical difference could be noted between the two. Figure 12 shows a series of specimens taken from a representative group at Las Peñas, a pueblo some 30 kilometers south of Jipi-japa in the province of Manabí on the western slopes of the Cerros de Colonche. All specimens were collected within a radius of 50 meters. Several of these individuals could easily be given specific names and in fact a plant very similar to number 4 of figure 12 which I collected from this same locality was donated to the Los Angeles County Arboretum where it was seen by Fowlie (1962) who suggested very strongly that it be named as a new species since it did not fit any of the descriptions contained in Mansfeld's monograph of the genus.

The problem became doubly significant when it was discovered that the same bees visit and pollinate all the various types of flowers indescriminately, regardless of their color or form. Bees of *Eulaema tropica* were observed passing from the flowers of the plant illustrated as number 4 of figure 12 to number 8 of the same figure. One bee visited a flower of number 4 and received pollinia on its thorax and then visited number 8. Another bee visited the same flower of number 4 and did not receive pollinia from that flower since it had already been triggered. He then flew to number 8 and did receive pollinia from a flower on that inflorescence. Both bees could then presumably fly to female flowers of either type and effect pollination. This behavior on the part of the bees is apparently the reason for the variation noted where populations of the two species come in contact. The importance however, is that variation is apparently permitted by a lack of selection for a particular type of flower since visits by bees were frequent for all types of flowers and no particular preferences were noted.

These species have evolved morphologically and physiologically to withstand a wide range of ecological habitats, from the xerophytic conditions of the coastal thorn forests to the wet tropical cloud-forests on the slopes of the Andes. Though having diverged in the past to form separate populations with very characteristic floral structures, the genus has maintained integrity of interfertility within all of its taxonomically definable species. Regardless of extremes in other floral structures, that part of the male flower critical in ensuring cross-fertilization, the column and its incumbent ejectable pollinarium, show remarkably little variation. Any consistant deviation from the condition that allows the successful ejection of the

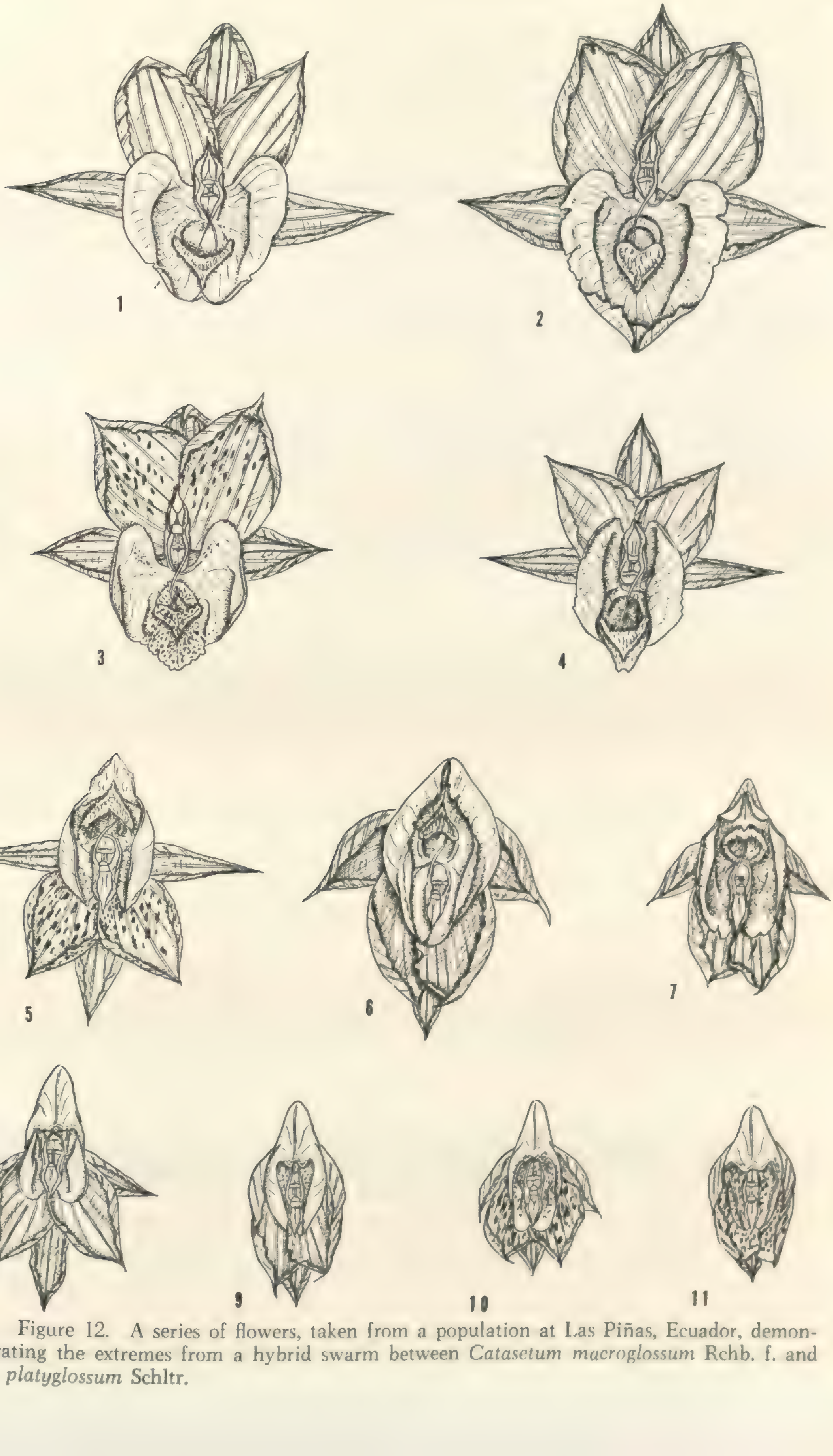

Figure 12. A series of flowers, taken from a population at Las Piñas, Ecuador, demonstrating the extremes from a hybrid swarm between *Catasetum macroglossum* Rchb. f. and *C. platyglossum* Schltr.

pollinarium and its precise deposition on the thorax of the bee would tend to eliminate that plant as a contributor to the gene pool of the population.

A situation which is apparently quite comparable to these populations and their hybrids in Ecuador occurs in Venezuela between *C. macrocarpum* A. Rich ex Kunth and *C. pileatum* Rchb. f. *Catasetum macrocarpum* is very similar to *C. macroglossum* and *C. pileatum* is quite close to *C. platyglossum*. A vast series of intermediates between these two concepts have been encountered and many were named by early taxonomists before the situation was understood. Plate 502 in *Lindenia* illustrates a series of these presumed hybrids which is quite similar to a comparable series which could be selected from the *C. macroglossum-C. platyglossum* series in the Cerros de Colonche.

Although *Mormodes* as a genus is amply distinct, the species boundaries or concepts within it are nearly nonexistent. Several recent papers, i.e., Teuscher (1954), Allen (1959) and Correll (1941) have pointed out the confusion involved but have done little to clarify the situation. There are three distinct kinds of *Mormodes;* those with strongly 3-lobed lips, those with obcordate lips and those with cordate lips. The factor which makes classification almost impossible, however, is that nearly every conceivable intermediate between these three basic types can be encountered. Not a great amount of information is as yet available but there may be definite, distinct populations of certain of these intermediate types. In other cases, there may be extremely variable populations demonstrating all types of variations on the three themes. This group promises to present formidable taxonomic problems, and there is the possibility that a simple clearcut account will not be possible.

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COMPARATIVE MORPHOLOGY OF THE OSMUNDACEAE

WALTER HEWITSON

Abstract

Thirteen species of the Osmundaceae were compared in the following respects: gross morphology of the fronds, sporangial structure, epidermal structure, leaf base anatomy and rhizome morphology. The purpose of comparing rhizome structure was to try to find anatomical criteria by which species could be identified in section, thereby providing a tool for the paleobotanist for determining affinities of fossil species. Disposition of sclerenchyma in the leaf bases is the only reliable character for this purpose. It is suggested that any descriptions of new living species or monographic treatments of the family should include this character. The subgenus Plenasium is unique in having two protoxylem groups in the leaf traces while they are still attached to the stem. The origin of this character is thought to be relatively recent and may have been derived through the subgenus Osmunda. Figures in the literature indicate that previous work on *Todea* and *Leptopteris* employed small rhizomes. Further study on larger rhizomes of these two genera may indicate the evolutionary pathway by which the stele in the family has undergone reduction in size and number of xylem bundles. Walter Hewitson, Department of Biology, Parsons College, Fairfield, Iowa.

Introduction

The Osmundaceae is a relatively small family of ferns that consists of three genera, *Osmunda, Todea* and *Leptopteris;* it contains about 21 species, depending upon how many of the described species are considered to be varieties of *Osmunda regalis* L. (Copeland, 1947; Christensen, 1906-34). Indications are that the family has been more abundant and more widely distributed in the geologic past; it can be traced back to the Permian by a series of well-preserved fossil stems.

Because of the fine fossil record, the small number of extant species and the isolated phylogenetic position of the family, the Osmundaceae has always been of interest to students of fern evolution. In particular, two questions have attracted a great deal of attention. The most difficult one concerns the origin of the family; for over 100 million years it has displayed a remarkable morphological constancy in those structures where living and fossil members can be compared. Because of this stability, a large phyletic gap exists between the most ancient forms and any supposed ancestors.

The second question concerns evolution within the family—in particular, evolution of the stele. Answers to this question have come from comparisons of fossil species with living species. An apparent failing in this method is that fossil stems have generally been compared with the three American species, *O. regalis*, *O. cinnamomea* and *O. claytoniana*, because of the inaccessibility of other species distributed in parts of the world remote from leading universities. It seems tenuous to base evolutionary theories for the family merely on the accidental juxtaposition of investigators and available material.

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* Part of an investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Andrews (1961) asserts:

> "it may be worth noting that Engler and Diels recognized 17 living species in their Syllabus der Pflanzenfamilien and since they have not all been studied critically, significant information may be forthcoming from studies of living plants as well as the fossils."

The main purpose of the present work, then, was to investigate as many species as possible in an attempt to relieve the uncertainty which will always exist so long as the morphology of some species in the family remains unknown.

MATERIALS AND METHODS

Source of the Material—One of the most difficult aspects of this problem was assembling material; the family has an almost cosmopolitan but discontinuous distribution. Thirteen species are included in the present study. The collectors and countries from which material came are summarized below.

Osmunda regalis L.		
	H. N. Andrews Jr.	New Hampshire, India
	J. W. Cliburn	Mississippi
	N. H. Nickerson	Massachusetts
O. japonica Thunb.		
	S. Hattori	Japan
	T. Kodama	Japan
	S. Miki & S. Kokawa	Japan
O. lancea Thunb.		
	S. Miki & S. Kokawa	Japan
O. cinnamomea L.		
	H. N. Andrews Jr.	New Hampshire
	T. H. Chung	Korea
	J. W. Cliburn	Mississippi
	N. H. Nickerson	Massachusetts
	K. Suvatabandhu	Thailand
O. claytoniana L.		
	H. N. Andrews Jr.	New Hampshire
O. javanica Blume		
	T. H. Chung	Korea
	N. Seneviratne	Ceylon
	K. Suvatabandhu	Thailand
O. vachellii Hook.		
	Herbarium of the Missouri Botanical Garden with permission of the Curator, R. E. Woodson Jr.	
O. bromeliaefolia (Pr.) Copel.		
	S. Hattori	Japan
	K. Tamari	Japan

O. banksiaefolia (Pr.) Kuhn		
	S. Miki & S. Kokawa	Japan
Todea barbara (L.) Moore		
	R. H. Michie	New Zealand
	N. Potts	New Zealand
	H. B. Ryeroft	South Africa
	S. L. Thrower	Australia
Leptopteris superba (Col.) Presl		
	G. T. S. Baylis	New Zealand
	G. Brownlie	New Zealand
	E. W. Curtis;	Botanic Gardens, Glasgow, Scotland
L. hymenophylloides (A. Rich.) Presl		
	G. T. S. Baylis	New Zealand
	E. W. Curtis	Scotland
	N. Potts	New Zealand
L. fraseri (Hook. et Grev.) Presl		
	R. H. Anderson	Australia
	S. L. Thrower	Australia

Treatment of the Material—All species in the Osmundaceae are terrestrial with erect, non-paleate stems. The stems are always deceptively bulky, being covered with a large mass of wiry roots and persistent leaf bases. The structure of such "stems" therefore demands special treatment. To obtain smooth stem sections one must trim away the roots and leaf bases. The rhizomes were then cut up into pieces from one to two centimeters in length in such a way that the proper sequence could be recognized and these pieces were softened in a 1: 1 solution of 48% hydrofluoric acid and 95% ethyl alcohol for a period of two weeks. At the end of this period the material was washed in running tap water for at least 24 hours. The material was then dehydrated in an ethyl alcohol series and embedded in celloidin according to Method 2 of Johansen (1940). Cross sections were made at 20 microns and longitudinal sections were cut at 10 microns. The trimmed-off leaf bases were treated in a similar manner. All sections were stained in 1% aqueous safranin and 0.5% fast green in 95% ethyl alcohol.

For studies of the leaf epidermis, pinnae were cleared in 5% NaOH and then transferred to 5% chloral hydrate to complete clearing. After washing, the pinnae were stained according to the ferric chloride-tannic acid method of Nevling (1951). Sporangia from herbarium sheets were rehydrated and mounted directly in glycerine jelly.

Observations

Osmunda can be distinguished from *Todea* and *Leptopteris* by the facts that in *Osmunda* the fertile pinnae are contracted with little or no vegetative lamina present and the pinnae are articulated at the point of attachment to the rachis. Diels (1898) recognized three subgenera in the genus *Osmunda*, subgenus Osmunda, subgenus Osmundastrum and subgenus Plenasium. Copeland (1947) pointed out that they are quite natural and could be treated as separate genera, but since the genus *Osmunda* is equally natural and not overly cumbersome,

Figure 1. Fronds of the subgenus Osmunda. A. *O. regalis*, B. *O. japonica*, C. *O. lancea*

Osmunda is retained as a single genus. The subgenera, however, are utilized in this study for convenience of description.

Gross Morphology of the Fronds

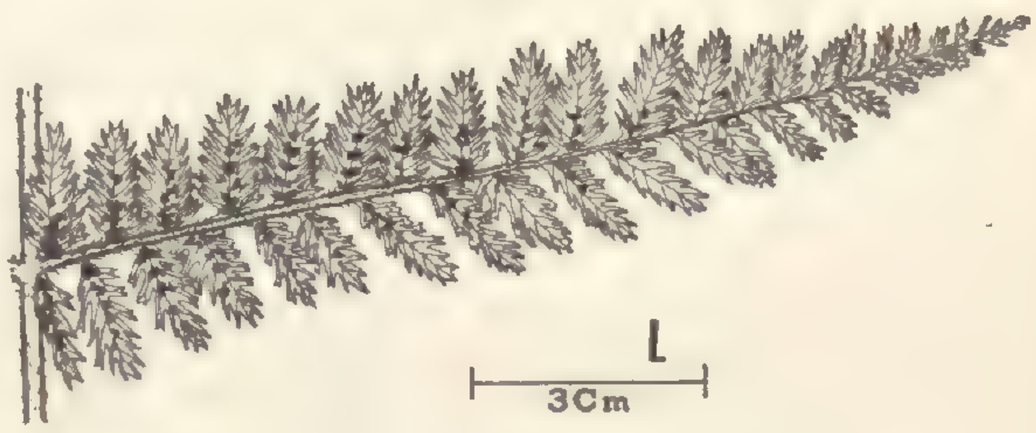
Subgenus Osmunda—This subgenus can be characterized by having bipinnate fronds. Disposition of fertile pinnae is also a character used to delimit the subgenera, but its importance is secondary to the method of frond branching. Thus, *O. lancea* is included in subgenus Osmunda because of its bipinnate fronds even though it resembles *O. cinnamomea* with completely dimorphic fronds. Subgenus Osmunda therefore demonstrates a transition from dimorphic pinnae on the same frond to completely dimorphic fronds. *Osmunda regalis* (Fig. 1A) typically displays only dimorphic pinnae with the fertile pinnae being apical. In *O. japonica* the position of the fertile pinnae is variable. It may resemble *O. regalis* with only the distal part of the frond fertile or it may be completely dimorphic. Finally, *O. lancea* (Fig. 1C) is usually completely dimorphic, occasionally incompletely dimorphic (Kokawa, personal communication).

Venation is an important character for defining fossil species from leaf impressions. In subgenus Osmunda it is difficult, if not impossible, to separate *O. regalis* (Fig. 4A) and *O. japonica* (Fig. 4B), but it is easy to separate both of them from *O. lancea* (Fig. 4C). In *O. regalis* and *O. japonica* the base of the pinnule is oblique and/or auriculate and the lowest pair of lateral veins are several times branched; the lateral veins along the pinnule are usually branched three times. In *O. lancea* the basal pair of lateral veins fork once; along the pinnule the lateral veins predominantly fork once or twice, rarely three times.

Subgenus Osmundastrum—When *O. lancea* is removed from this subgenus, Osmundastrum is a natural group of two species, *O. cinnamomea* and *O. claytoniana*. The fronds of both species are once pinnate and the pinnae are deeply pinnatifid. The two species are easily distinguished in the fertile condition because *O. cinnamomea* (Fig. 2D) has completely dimorphic fronds while *O. claytoniana* has dimorphic pinnae on the same frond with the fertile pinnae usually being attached along the midpoint of the rachis. *Osmunda cinnamomea* is more hairy than *O. claytoniana*, but both species lose most of their hairiness as they mature.

When deprived of the fertile fronds, one has a more difficult time distinguishing the two species because the vegetative differences are subtle. *Osmunda cinnamomea* has a sub-coriaceous texture; *O. claytoniana* is more herbaceous. Shape of the ultimate pinnae is slightly different. The apices of the pinnules in *O. cinnamomea* (Fig. 4D) are often tapered and the margins are irregular; *O. claytoniana* (Fig. 4E) has a blunter more rounded apex and the margin is smooth and full. Venation is not a workable character for separating the two species, although it is sufficiently unique to describe the subgenus.

Subgenus Plenasium—The number of species in this subgenus is questionable, but they all share the common characteristic of once-pinnate fronds. *Osmunda javanica* (Fig. 3F) bears its fertile pinnae about in the middle of the rachis with sterile pinnae on either side; the margins of the pinnae may be toothed or entire.



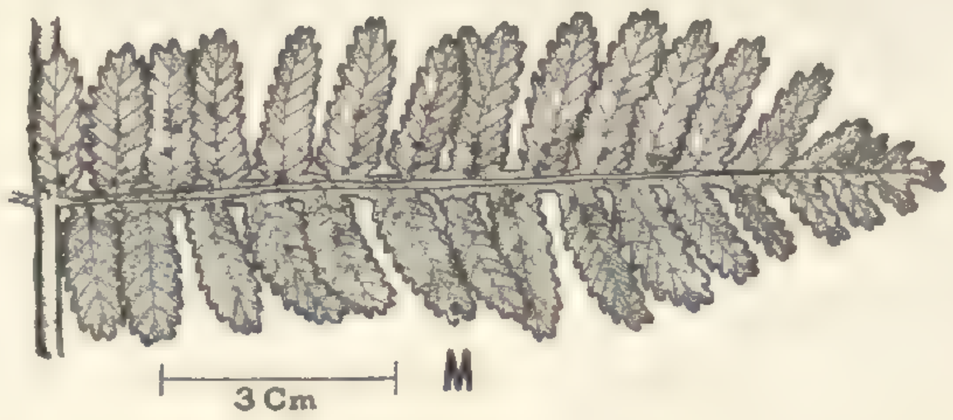


Figure 2. D. E. Fronds of the subgenus Osmundastrum, D. O. *cinnamomea*, E. O. *claytoniana*, J. *T. barbara*, K. *L. superba*, L. *L. hymenophylloides*, M. *L. fraseri*.

Figure 3. Fronds of the subgenus Plenasium, F. O. *javanica*, G. O. *vachellii*, H. O. *bromeliaefolia*, I. O. *banksiaefolia*.

The key characters for O. *vachellii* (Fig. 3G) are basal fertile pinnae and entire vegetative pinnae. *Osmunda bromeliaefolia* (Fig. 3H) has narrow, toothed pinnae borne oppositively or subopposite on the rachis; O. *banksiaefolia* (Fig. 31) bears its wider more coarsely toothed pinnae alternately. Both have their fertile pinnae disposed along the middle of the rachis.

Venation nicely separates the species in Plenasium from one another as well as from the other species in the family. *Osmunda javanica* (Fig. 4F) is more regular in its venation than O. *vachellii* (Fig. 4G). The vein to the left in Figure 4F occurs repeatedly for about three-fourths of the length of the pinna in O. *javanica* and the vein to the right continues nearly to the apex of the pinna where the vein type becomes still simpler and once branched. In O. *vachellii* the method of branching of the lateral veins is variable all along the length of the pinna. Both species are simpler in venation than either O. *bromeliaefolia* or O. *banksiaefolia*. In O. *bromeliaefolia* (Fig. 4H) there are two major branches of the lateral veins; in O. *banksiaefolia* (Fig. 4I) there are three major branches.

Todea—The monotypic *Todea* may be recognized by its coriaceous, bipinnate fronds with dense clusters of sporangia borne on the abaxial surface of typical vegetative pinnae (Fig. 2J). The lateral veins of the pinnules may be forked once or unbranched.

Leptopteris—The unifying character for this genus which separates it from *Todea* is the filmy habit. All species are bipinnate, but differ in the degree to which the pinnules are incised. *Leptopteris superba* (Figs. 2K, 4K) is most deeply cut and the rachis is densely pubescent. *Leptopteris hymenophylloides* (Figs. 2L, 4L) is not as deeply cut; the cutting is sharp, not rounded and the rachis is less pubescent. Another distinguishing character is that in *L. superba* the basal pinnae are much shorter than the ones immediately above; in *L. hymenophylloides* the basal pinnae and those above are nearly of equal length. Both species are closely related and it is often difficult to tell them apart because they may grade into one another. Allen (1961) believed that a third species in New Zealand, *L. marginata*, really represents an intergrade between these two species. *Leptopteris fraseri* is the least incised of the species considered here (Figs. 2M, 4M). Venation (Figs. 4, K, L, M) is the simplest for the whole family.

Sporangia

Sporangial structure has been little used for specific delimitation in the Osmundaceae. While the structure is reliable for recognizing the family, it is too variable at the species level for classification purposes. This variability in structure could be expected, since the family is considered to be a primitive one among the ferns and there is a trend from variability to a precise dehiscence mechanism when the lower and higher ferns are compared.

Common to the family is a transverse rudimentary annulus of thick-walled cells. Depending upon the size of the sporangia and the number of cells in it, the annulus may extend as much as half way around the sporangium or less. Dehiscence is vertical. The position of the annulus in relationship to the sporangium stalk can be used taxonomically to delimit *Leptopteris*. In *Leptopteris* the annulus

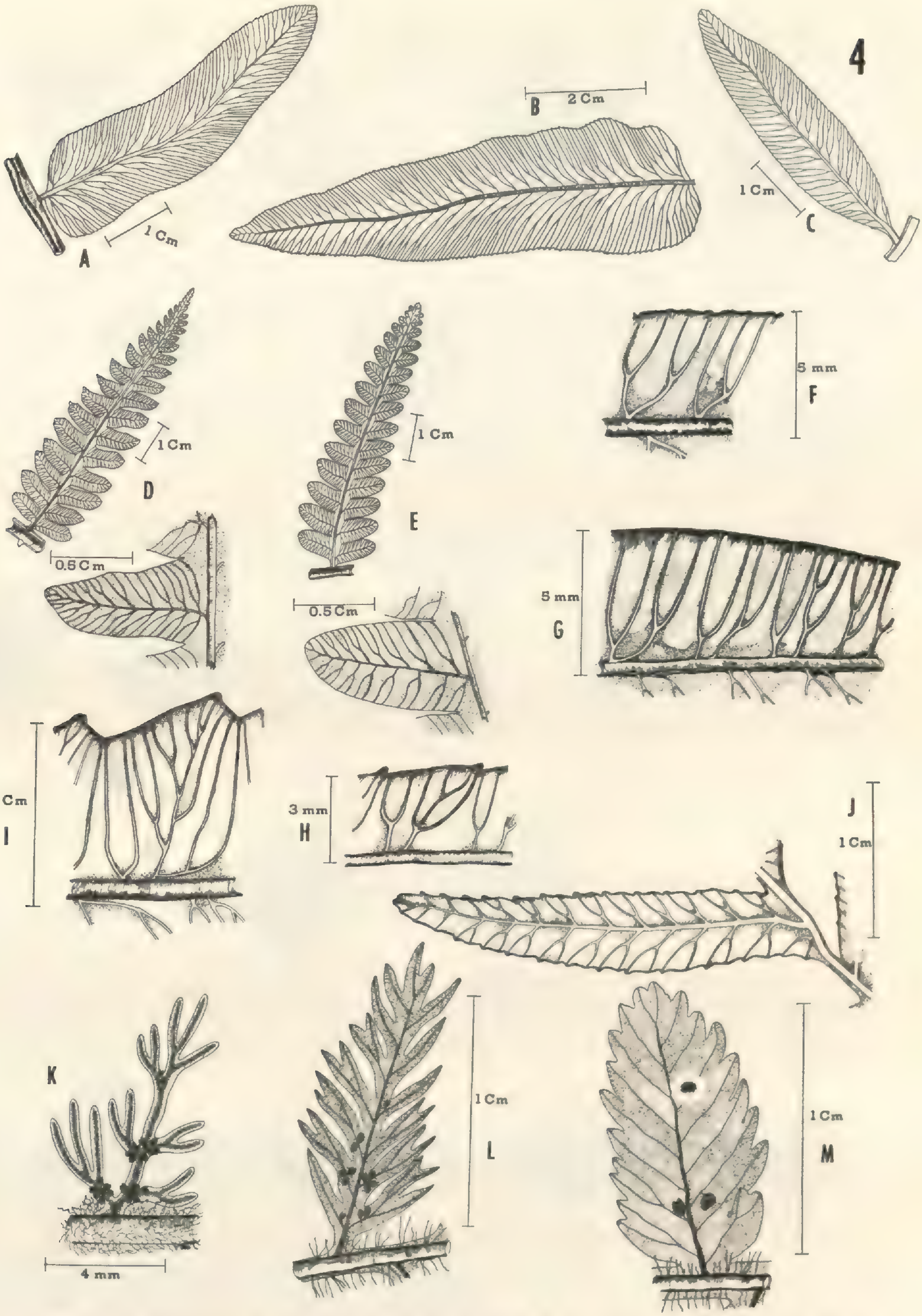


Figure 4. Venation of the species. A. *O. regalis*, B. *O. japonica*, C. *O. lancea*, D. *O. cinnamomea*, E. *O. claytoniana*, F. *O. javanica*, G. *O. vachellii*, H. *O. bromeliaefolia*, I. *O. banksiaefolia*, J. *T. barbara*, K. *L. superba*, L. *L. hymenophylloides*, M. *L. fraseri*.

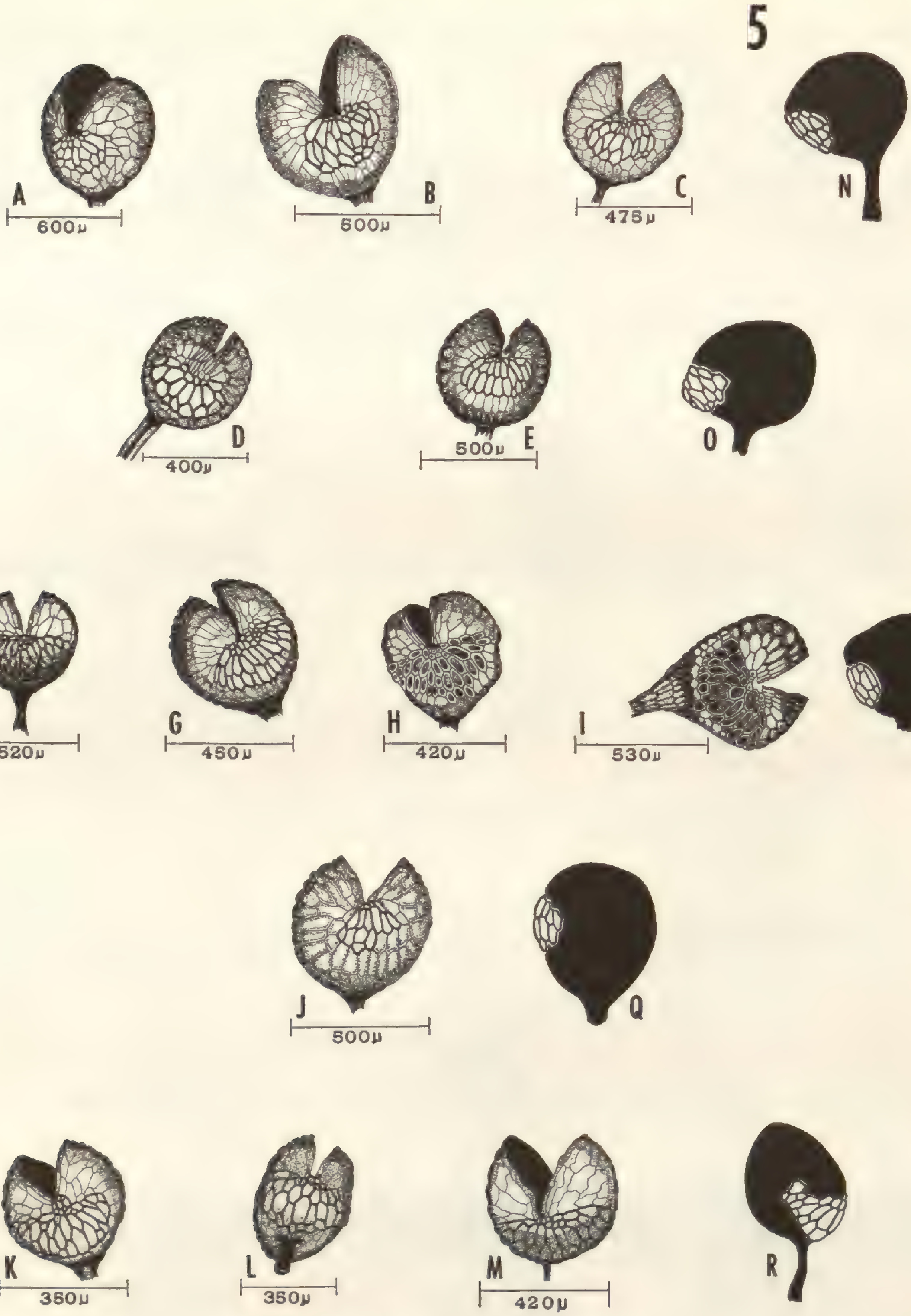


Figure 5. Sporangial structure. A. O. *regalis*, B. O. *japonica*, C. O. *lancea*, D. O. *cinnamomea*, E. O. *claytoniana*, F. O. *javanica*, G. O. *vachellii*, H. O. *bromeliaefolia*, I. O. *banksiaefolia*, J. *T. barbara*, K. *L. superba*, L. *L. hymenophylloides*, K. *L. fraseri*.

N to R. Distance of annulus from stalk. N. Subgenus Osmunda, O. Subgenus Osmundastrum, P. Subgenus Plenasium, Q. *Todea*, R. *Leptopteris*.

touches the stalk or at most is one cell removed from it (Fig. 5R). *Todea*, closest taxonomically to *Leptopteris*, demonstrates the opposite extreme in the family with the annulus being farthest away from the stalk (Fig. 5Q). Osmunda (Figs. 5, N, O, P) is intermediate between these extremes.

Below is a table representing a summary of the variation ranges found within the species. "Diameter" indicates the greatest transverse diameter in microns; "# cells broad" is the transverse length of the annulus; "# cells deep" is the vertical width of the annulus; "# cells" indicates the number of cells in the annulus, disregarding the small cells near the stomium for the purpose of being more objective.

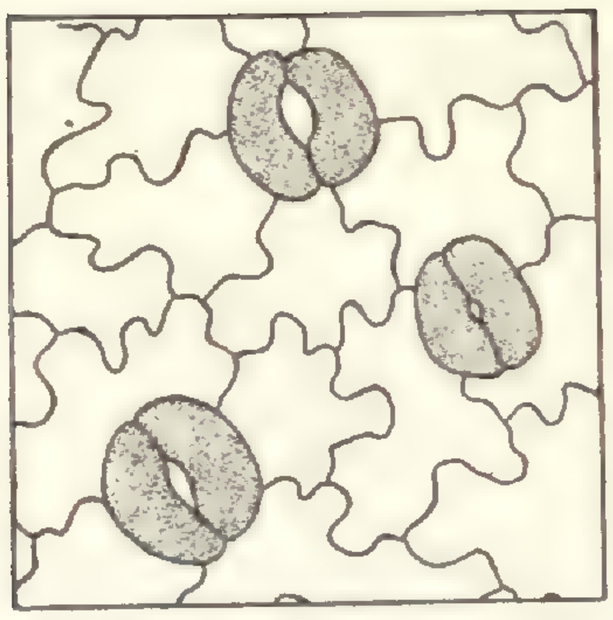
Species	Diameter	# Cells Broad	# Cells Deep	# Cells
O. *regalis*	550-700	7-10	2-3	16-29
O. *japonica*	420-500	10-14	2-4	26-34
O. *lancea*	420-560	9-12	2-4(5)	27-40
O. *cinnamomea*	420-480	8-10	2-3	16-25
O. *claytoniana*	420-550	10-14	2-3	22-32
O. *javanica*	420-550	10-14	2-4	26-36
O. *vachellii*	420-580	8-13	2-4	25-35
O. *bromeliaefolia*	420-550	7-14	2-4	21-31
O. *banksiaefolia*	420-590	12-15	2-4(5)	28-36(40)
T. barbara	460-630	4-12	2-3	9-24
L. superba	330-420	10-16	2-3	25-31
L. hymenophylloides	380-420	11-13	2-3	25-33
L. fraseri	380-550	11-15	2-4	26-40

By far the most variable species are O. *regalis* and *T. barbara.* Both have the largest sporangia for the family, usually near the upper limits shown in the table (about 600 microns). *Todea* has the most variable annulus structure for the family. The same pinna may bear sporangia with annuli having as few as 9 cells and sporangia with well-developed annuli having as many as 24 cells. *Osmunda regalis* may show almost as much variation and even more if *O. japonica* is treated as a variety.

The remaining species show less variability than the preceding, but enough to make generalizations impractical. Thus, the genera and subgenera only suggest the following weakly defined characteristics:

Subgenus Osmunda—Annulus 2-4 cells deep with as few as 16 to as high as 40 cells, somewhat shield- or oval-shaped, extending about a third of the way around the sporangium or less (Figs. 5, A, B, C).

Subgenus Osmundastrum—Annulus mostly 2(3) cells deep with about 16 to 30 cells, oblong and extending less than half way around the sporangium, but more than in subgenus Osmunda; *O. cinnamomea* with consistently the smallest sporangia for *Osmunda* (less than 500 microns in diameter), (Figs. 5, D,E).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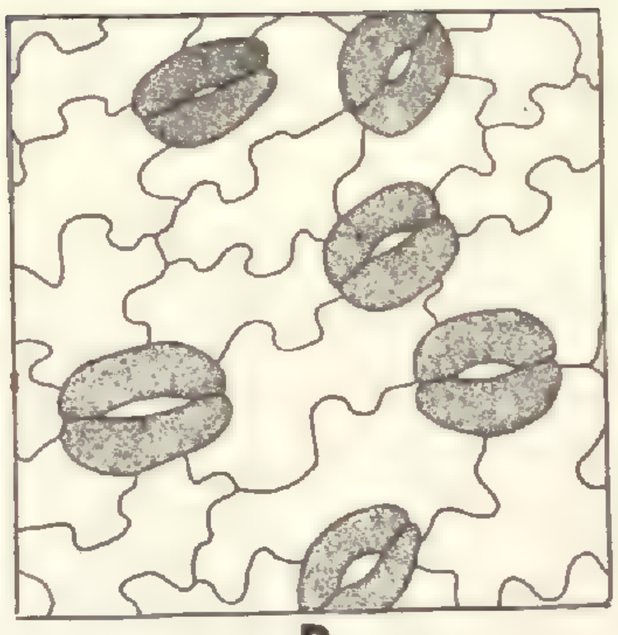
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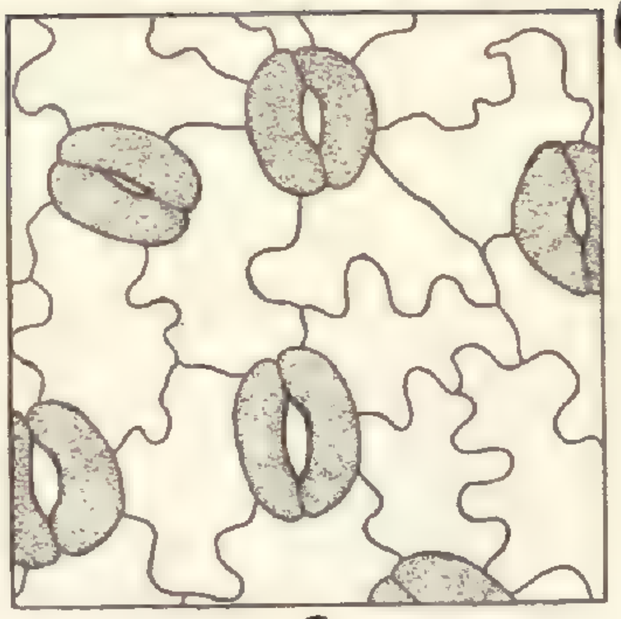
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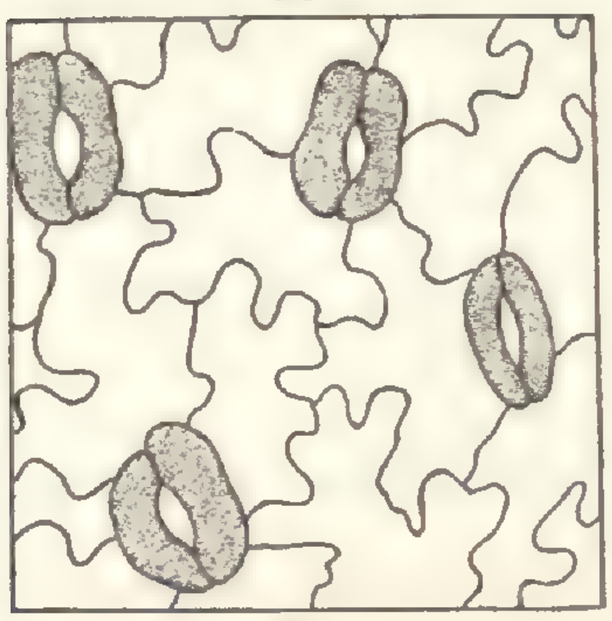
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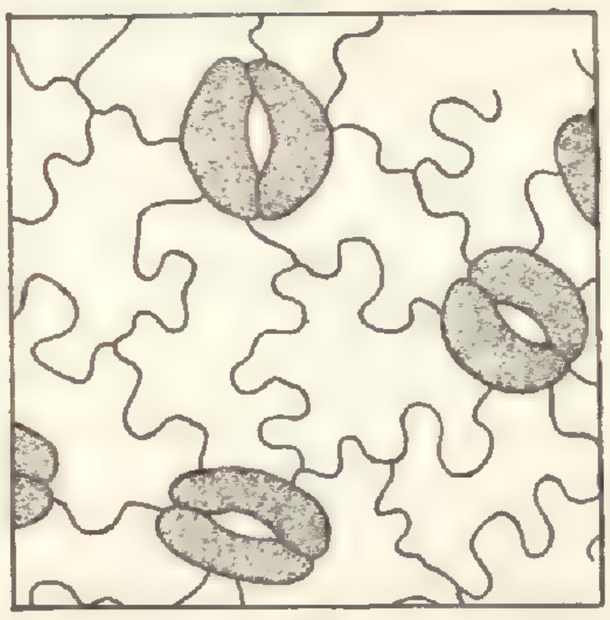
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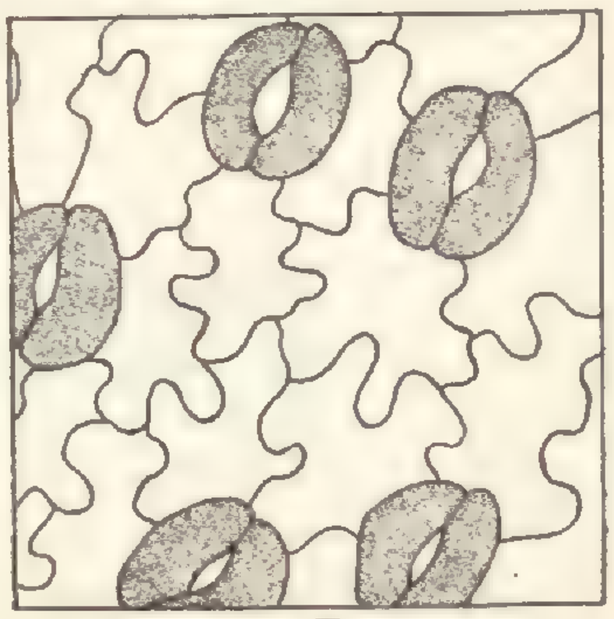
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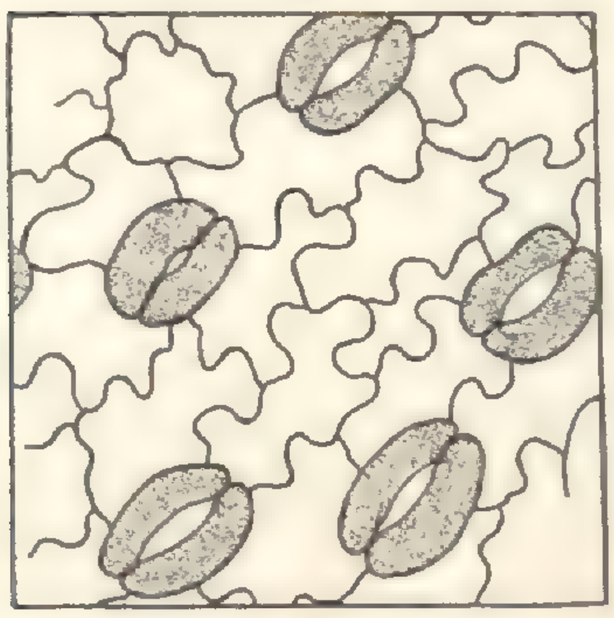
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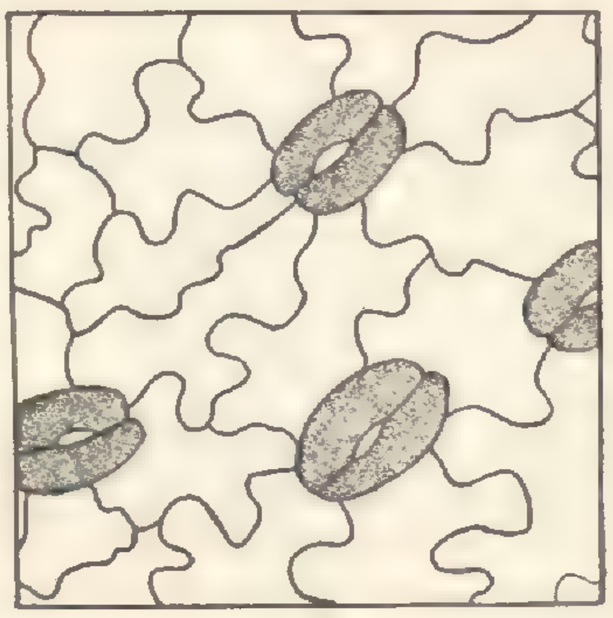
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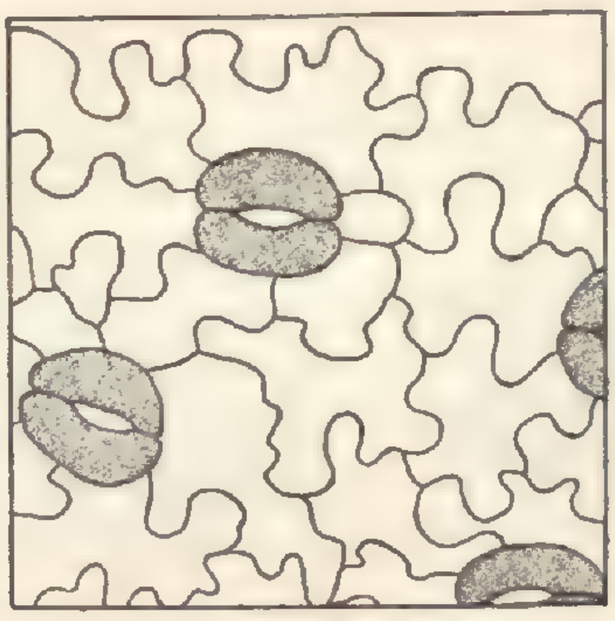
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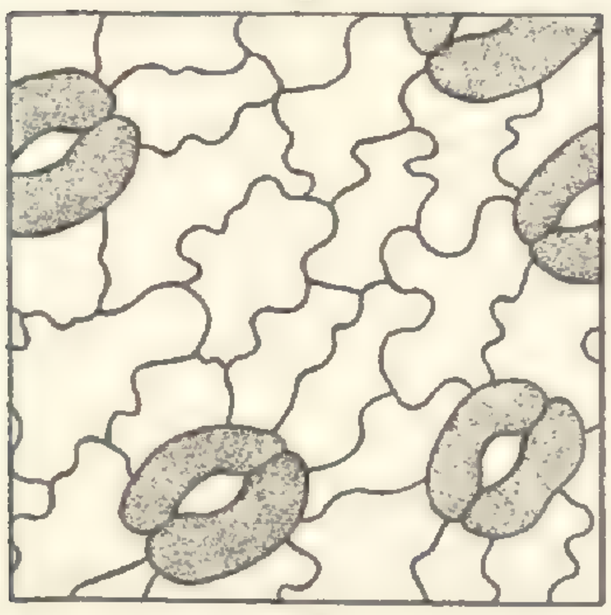
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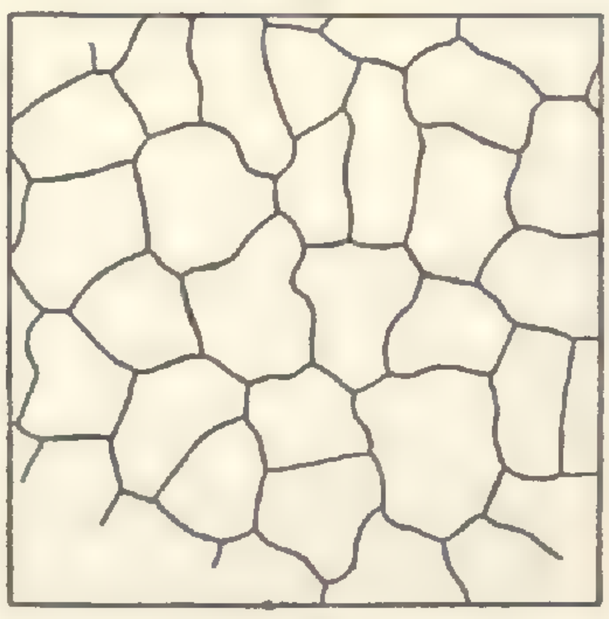
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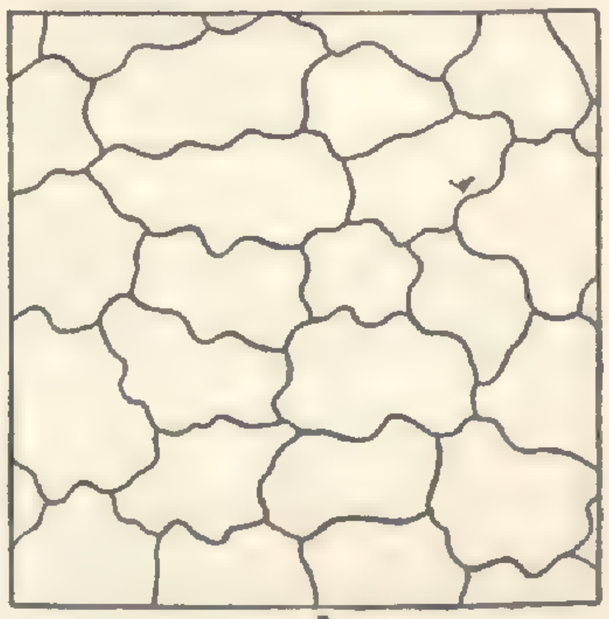
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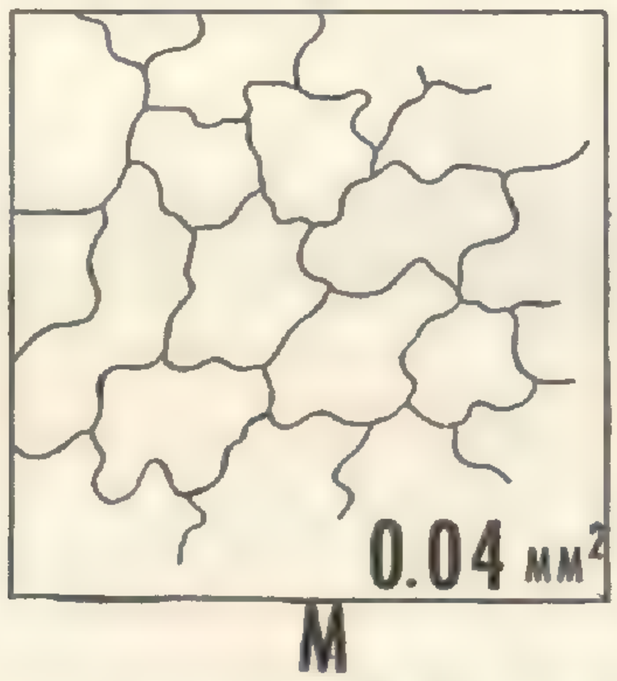


M

Figure 6. Abaxial epidermal structure. A. *O. regalis*, B. *O. japonica*, C. *O. lancea*, D. *O. cinnamomea*, E. *O. claytoniana*, F. *O. javanica*, G. *O. vachellii*, H. *O. bromeliaefolia*, I. *O. banksiaefolia*, J. *T. barbara*, K. *L. superba*, L. *L. hymenophylloides*, M. *L. fraseri*.

Subgenus Plenasium—Annulus 2-4 cells deep with a relatively higher number of cells than in subgenus Osmunda; see text (Figs. 5, F,G,H,I).

Todea—Annulus 2-3 cells deep and quite variable in numbers of cells (9-24), oval-shaped and extending about one-fourth of the way around the sporangium, far removed from the stalk; sporangia large (about 600 microns), (Figs. 5, J,Q).

Leptopteris—Annulus 2-3 cells deep with a relatively high number of cells (about 30), elongate and extending at least half way around the sporangium, touching or one cell removed from stalk; sporangia smallest for the family (about 420 microns), (Figs. 5, K,L,M,R).

Epidermal Structure

The structure of the epidermis has been of great value for determining past and present phyletic lines, particularly in the Gymnosperms. In the Osmundaceae it cannot be utilized for identification of species with any surety, but it can be used as a unifying character for the family. The family lacks stomata on the adaxial surface of the frond and the epidermis consists of typical jig-saw-puzzle-shaped cells. The configuration of the epidermal cells on the abaxial surface of the frond is consistent for *Osmunda* and *Todea* (Figs. 6, A-J). Only *Leptopteris* (Figs. 6, K,L,M) can be recognized with certainty because it lacks stomata on either surface of the frond, an indication of its filmy habit.

Leaf Bases

Kidston and Gwynne-Vaughan (1907) attempted to establish anatomical criteria whereby living species of the Osmundaceae could be identified in section for the purpose of comparison with fossil species. The only useful character they could find was the arrangement of sclerenchyma strands in the leaf bases.

Subgenus Osmunda—Of the three species in this subgenus, Kidston and Gwynne-Vaughan studied *O. regalis*. Figure 7A of *O. regalis* agrees with their description in all details. *Osmunda japonica* (Fig. 7B) is quite similar to *O. regalis;* the only difference is that *O. japonica* has a number of scattered sclerenchyma strands just outside of the continuous ring of selerenchyma, and these are lacking in *O. regalis*. *Osmunda lancea* (Fig. 7C) differs from these two species in that there is not a long continuous patch of sclerenchyma extending out into the wings.

Subgenus Osmundastrum—This subgenus is most easily recognized because the continuous ring of sclerenchyma around the leaf trace is heterogeneous. That is, most of the ring has a relatively thin-walled sclerenchymatous cell type with the lumina apparent, but patches of sclerenchyma with thick walls and occluded lumina occur in the ring. *Osmunda claytoniana* (Fig. 7E) has two of these patches and *O. cinnamomea* (Fig. 7D) has three. *Osmunda claytoniana* further differs in having a single strand of sclerenchyma in the wings, a continuous band of sclerenchyma in the bay of the C-shaped leaf trace and isolated strands scattered within the rings; *O. cinnamomea* has scattered sclerenchyma in the wings, two distinct patches on the adaxial side of the trace and no isolated strands scattered inside the ring.

Subgenus Plenasium—This subgenus can be characterized by the presence of

scattered sclerenchyma strands within the continuous ring. *Osmunda javanica* (Fig. 7F) and *O. vachellii* (Fig. 7G) are practically indistinguishable except that *O. javanica* has two more strongly developed strands in the wings near the continuous ring. Such a slight difference would not appear to be significant. Figures 7H (*O. bromeliaefolia*) and 7I (*O. banksiaefolia*) seem to indicate that these two species are distinguishable on the basis of the sclerenchyma in the bay of the C-shaped trace. In *O. bromeliaefolia* the sclerenchyma is continuous, while in *O. banksiaefolia* it is interrupted. The material of *O. bromeliaefolia* was poorly preserved, however, and Ogata (1933) indicated that the sclerenchyma in this species is also interrupted. This appears quite reasonable to me on the basis of anatomical similarities for other characters. A minor difference is that in *O. bromeliaefolia* there are two slightly stronger sclerenchymatous patches near the ring.

Todea—Todea barbara, like Plenasium, has sclerenchyma strands scattered within the ring (Fig. 7J), but it differs from Plenasium in lacking any strongly-developed sclerenchyma on the adaxial side of the trace.

Leptopteris—Leptopteris differs from its nearest ally, Todea, in lacking sclerenchyma scattered inside of the ring and by having a band of sclerenchyma on the adaxial side of the leaf trace. Further, the ends of the trace in *Todea* are recurved to form a hook (Fig. 7J) while the hook is lacking in *Leptopteris.* Figure 7K is of *L. superba and* 7L is of *L. hymenophylloides.* The figures indicate that *L. hymenophylloides* has four strongly developed strands in each wing while *L. superba* has one strong strand and a number of poorly developed patches scattered in each wing. These figures are exactly the opposite of those figured by Kidston and Gwynne-Vaughan (1907, Plate VI, figs. 9 & 10). I feel reasonably certain that there has not been a mixup in my material. These two species are so close to one another (frequent intergrades are found) that this much variation might be possible. *Leptopteris fraseri* (Fig. 7M) differs from these two species in having weakly developed sclerenchyma scattered throughout the wings.

Rhizomes

The morphology of the rhizome is a good measure of naturalness for the Osmundaceae. It is consistent for the family and unique for the ferns so that anyone who has ever handled the rhizome of just one species would certainly know when he is dealing with an osmunda. The rhizome is sheathed with a mass of wiry roots and persistent leaf bases. Both leaf bases and roots are liberally supplied with sclerotic tissue, most likely indicating why there is a rich fossil record for the family.

Cortex—Strictly speaking, the roots and the leaf bases should not be considered a part of the stem. The actual limit of the stem is the periphery of the cortex. However, the leaf bases are frequently so closely packed and appressed and the cortex so poorly defined that it is difficult to interpret the dimensions of the stem. This difficulty is associated with *Todea* and *Leptopteris;* in *Osmunda* the limits of the cortex are usually well-defined.

The cortex is differentiated into outer and inner zones and the line of demarcation is usually quite sharp. Composed of elongate sclerotic cells with simple,

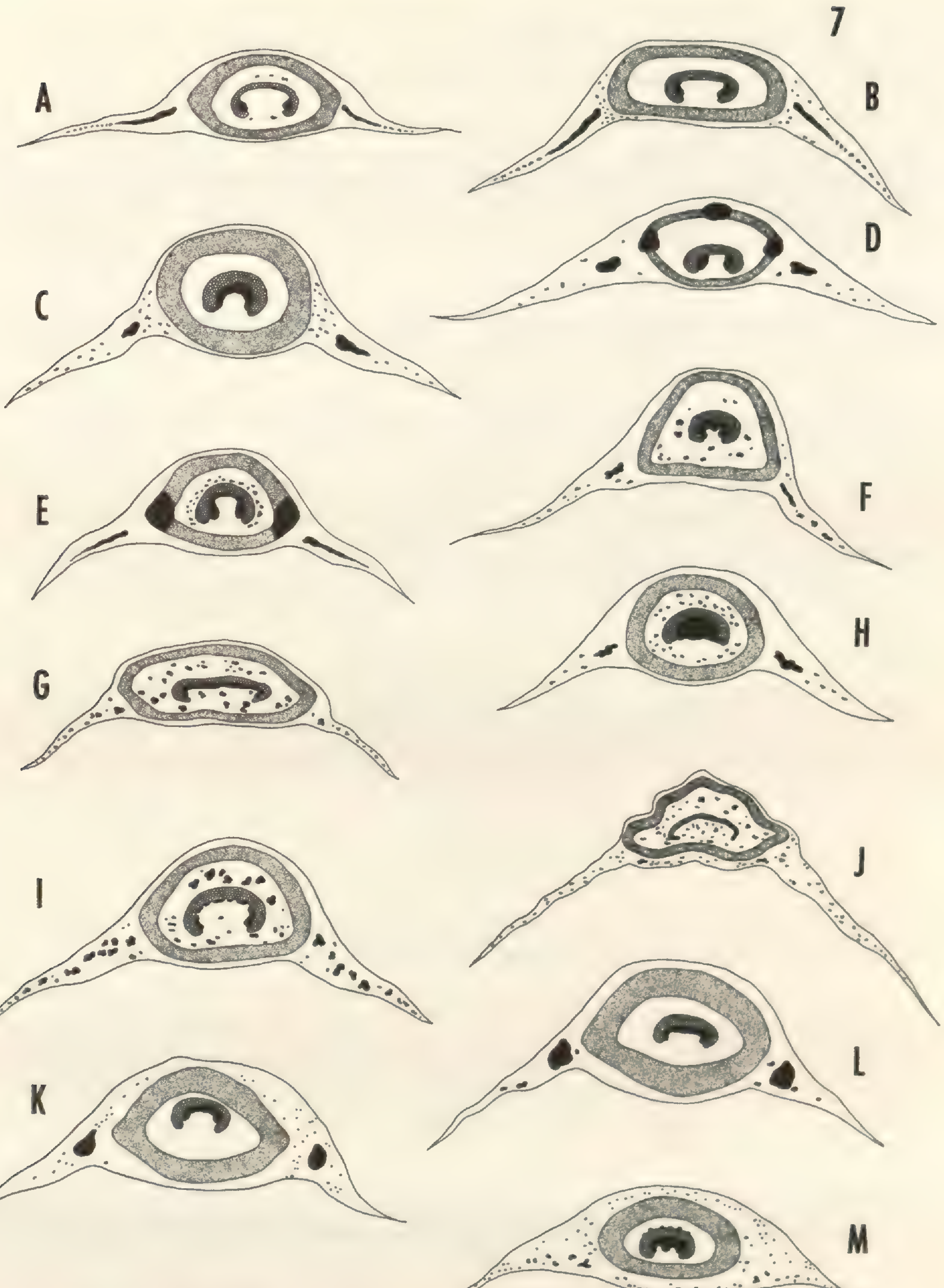


Figure 7. Disposition of sclerenchyma in the leaf bases. Black and heavy shading represent sclerenchyma. Traces are cellular. Diagrammatic and not drawn to relative sizes. A. *O. regalis,* B. *O. japonica,* C. *O. lancea,* D. *O. cinnamomea,* E. *O. claytoniana,* F. *O. javanica,* G. *O. vachellii,* H. *O. bromeliaefolia,* I. *O. banksiaefolia,* J. *T. barbara,* K. *L. superba,* L. *L. hymenophylloides,* M. *L. Fraseri.*

oval or slit pits, the outer cortex is always most extensive, sometimes reaching 3 mm in thickness. The inner parenchymatous cortex, which is pentagonal in outline as seen in cross-section, seldom becomes as much as one mm thick.

Both the outer and inner cortex are interrupted by the diagonally outward- and upward-departing leaf traces and by numerous roots. The leaf traces are C-shaped with the opening directed adaxially and are spirally arranged. Phyllotaxy for the mature rhizome is 8/21. In younger rhizomes or toward the base of mature rhizomes the 5/13 fraction can also be observed. Cribbs (1920) reported fractions of 2/5 and 3/8 for sporelings of *T. barbara*.

Because the leaf traces are so numerous, stages in departure of a trace from the time it leaves the stele until the time it leaves the cortex can be followed in one cross-section of the stem. Figure 7 indicates that in the leaf bases of all the species there is a sclerotic ring surrounding the trace. The trace as it passes through the inner cortex is surrounded by parenchymatous tissue. As it enters the outer cortex the trace and some of the inner cortical parenchyma become surrounded by sclerenchyma. When the trace leaves the outer cortex it carries with it some of the sclerenchyma in the form of a continuous ring.

The development of this ring can be useful for distinguishing *Osmunda* from *Todea* and *Leptopteris*. In *Osmunda* the outer cortex is homogeneous in its cell type so that the ring does not become apparent until it protrudes from the outer cortex. But in *Todea* and *Leptopteris* the outer cortex is composed of two cell types. The ring consists of thick-walled cells with small, almost occluded lumina while the surrounding tissue of the outer cortex consists of thinner-walled sclerotic cells with larger more apparent lumina. Thus, in *Osmunda* the sclerotic ring of the leaf base is not apparent while the trace is in the outer cortex (Fig. 8); in *Todea* and *Leptopteris* the ring is obvious (Figs. 9, J,K,L). *Osmunda cinnamomea* is unique and can always be recognized in cross-section because a nest of sclereids develops adaxial to the trace while it is still in the inner cortex (Fig. 8, D). *Todea* and *Leptopteris* may sometimes display a weak nest of similar sclereids.

Arnold (1952) used as a diagnostic feature for fossil species the number of leaf traces in an area of 2.5 cm^2. Such an area includes the free leaf bases outside the cortex. For living material these bases must be trimmed away to get smooth sections. The following summary, then, is based on the number of traces found only in the stem itself. To be counted the trace had to be free from the stele and the outer limits of the leaf base could not be distinct from the outer cortex. Thus, in Fgure 8C there are 9 traces.

Osmunda cinnamomea and *O. claytoniana* are easily recognized because of the relatively high number of traces in the stem, particularly in the inner cortex (up to 12). Other species regularly have about 3 traces in the inner cortex, rarely more. Exceptional in this respect is the subgenus Plenasium. The inner cortex is quite thin, so that most often no traces can be observed in the inner cortex; sometimes one may be observed.

The number of traces in the stem depends upon the angle of the departing traces and the size of the stem. In subgenus Osmunda the leaf traces depart at

	Number of Traces		
	Entire Cortex	*Inner Cortex*	*Outer Cortex*
O. regalis	8-14	2-3	5-11
O. japonica	8-14	2-4	5-11
O. lancea	12-20	1-5	11-15
O. cinnamomea	11-27	4-12	7-15
O. claytoniana	15-20	4-7	11-13
O. javanica	3-7	0-1	3-6
O. vachellii	8	1	7
O. bromeliaefolia	4-8	0-1	4-8
O. banksiaefolia	4	0	4
T. barbara	6-12	2-5	3-8
L. superba	9-27	2-8	6-20
L. hymenophylloides	4-15	0-2	4-13
L. fraseri	4-8	1-3	3-7

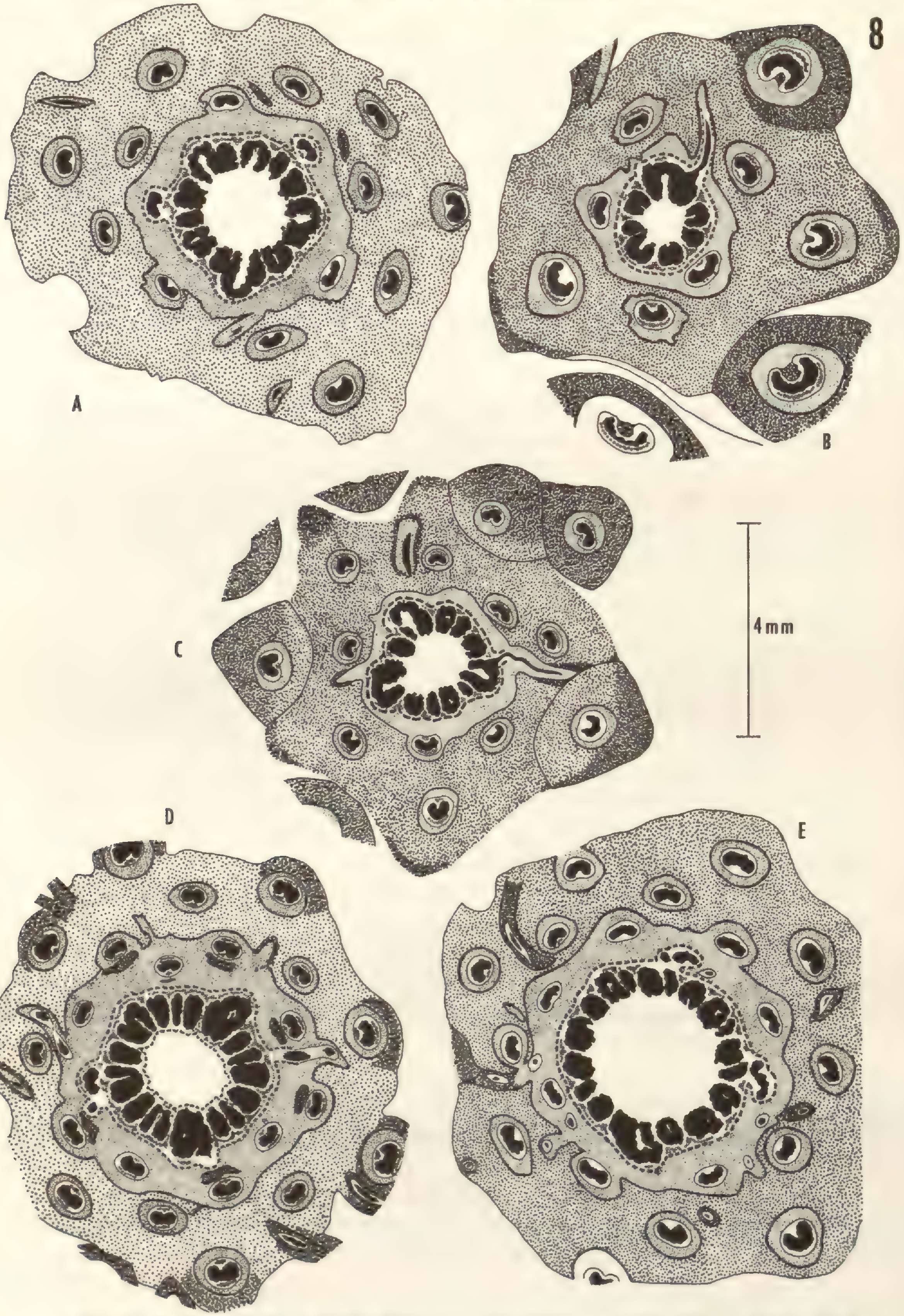
angles ranging from 25 to 40°. The traces in Osmundastrum leave the stele at relatively steep inclinations of 15-25°, thereby partly accounting for the relatively high numbers of traces in *O. cinnamomea* and *O. claytoniana*. The angle of departure for Plenasium is 30-45°. This angle is reflected in the regular occurrence of oblique sections of leaf traces when the stem is sectioned transversely. The angle for *Todea* and *Leptopteris* is about 30°.

The number of traces in the stem of *L. superba* (9-27) is a fairly good indication that the size of the rhizome has a great deal to do with the interpretation of anatomical structure for this genus. From figures in the literature it is apparent that past work done on this genus was carried out on relatively small rhizomes. The high number of traces for *L. superba*, which seems so out of line in comparison to the rest of the genus, comes from a single fairly large rhizome. Smaller rhizomes agree closely with the other *Leptopteris* species.

Endodermis—The endodermis in the Osmundaceae is most often a tissue that must be identified by its position rather than by its structure; it is a uniseriate layer of cells lying between the cortex and the pericycle. Usually it is filled with starch grains and tannins (as revealed by I_2KI and 10% $FeCl_3$) so that the characteristic endodermal thickenings on radial walls are obscured. These thickenings can be somewhat intensified by treatment with phloroglucinol in 18% HCl. In preparations where the protoplast has pulled away from the cell wall the radial thickenings can easily be seen.

In all rhizomes examined, with the exception of *O. cinnamomea*, the endodermis was a completely continuous ring. Where roots and leaf traces depart from the stele their endodermal layers join with that of the stem, never causing an interruption. Faull (1901) reported gaps in the endodermis in regions where rhizomes bifurcate for *O. cinnamomea*. Such ramular gaps did not occur in my material.

Osmunda cinnamomea has always been the center of phyletic arguments for the Osmundaceae because it is unique in regularly (not always) possessing an external as well as an internal endodermis. In Faull's material, both rings some-



Figures 8. Cross sections of the rhizomes. Semi-diagrammatic. Xylem, black. Endodermis, broken lines. Inner cortex, light shading. Outer cortex, dark shading. A. O. *regalis*, B. O. *japonica*, C. O. *lancea*, D. O. *cinnamomea*, E. O. *claytoniana*.

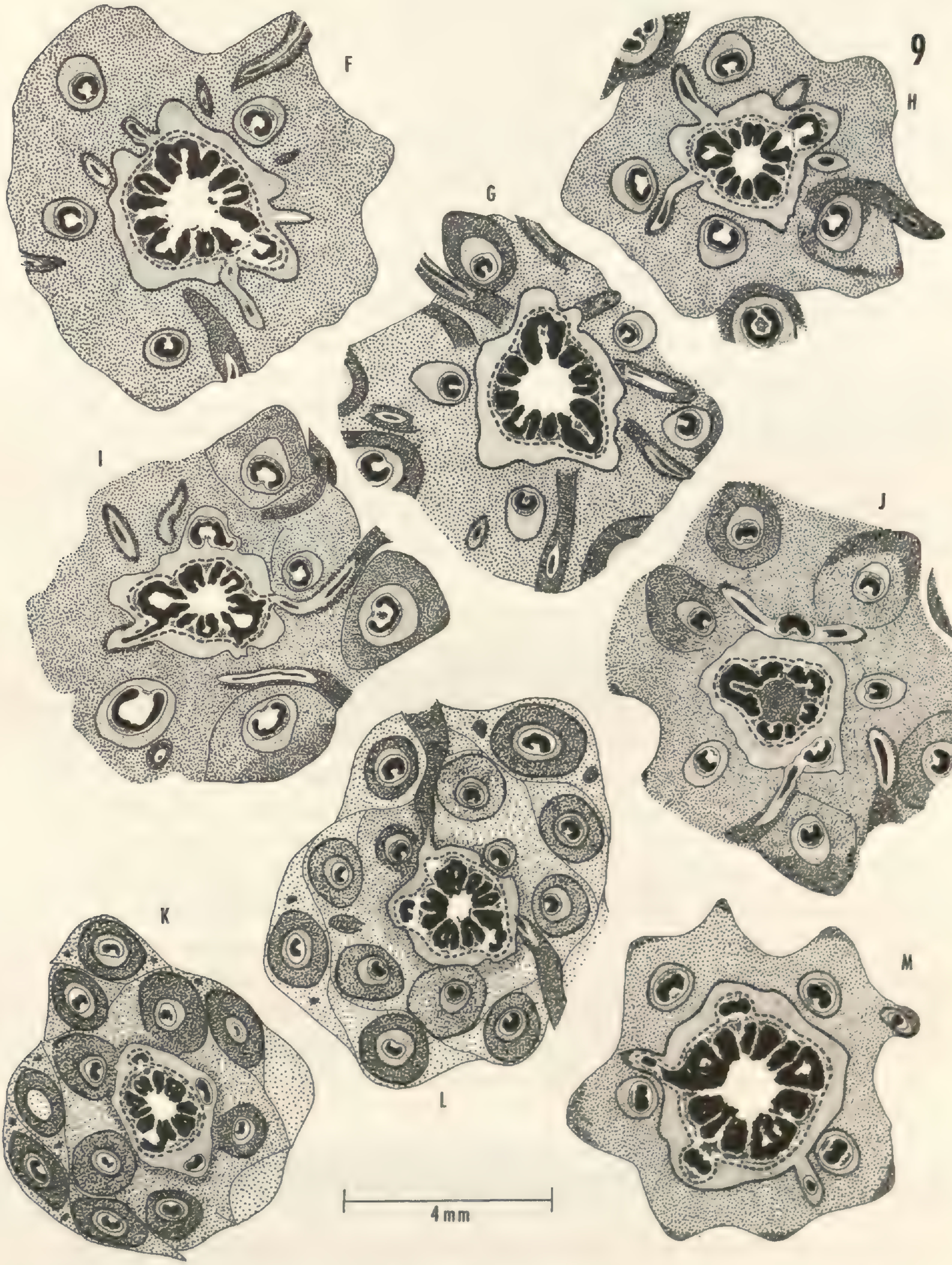


Figure 9. Cross sections of the rhizomes. Semi-diagrammatic, Xylem, black. Endodermis, broken lines. Inner cortex, light shading. Outer cortex, dark shading. F. *O. javanica,* G. *O. vachellii, H. O. bromeliaefolia,* I. *O. banksiaefolia,* J. *T. barbara,* K. *L. superba,* L. *L. hymenophylloides,* M. *L. fraseri.*

times joined together through the ramular gaps. The only place I have seen the rings come into contact is through the xylic gaps into which the rings dip (Fig. 11) and even then, the contact occurs only in branching regions of the rhizomes. Seward and Ford (1903) mentioned a sporadic, longitudinally discontinuous internal endodermis in *L. hymenophylloides* but this feature was not present in my material.

Pericycle—The pericycle is an enigmatic tissue for the vascular plants, being variously developed in different groups and in different organs. In the Osmundaceae it is present in all of the species I examined and is poorly- or well-developed according to the material examined. Generally the pericycle consists of one to three layers of prosenchymatous cells. These cells may have their long axes oriented vertically, tangentially or diagonally. As in other groups where it is well-defined, the pericycle is the point of origin for roots. Once the pericycle cells have differentiated, roots no longer arise from them. That is, roots originate in the young portions of the rhizome near the apex and not from older mature portions far removed from the apex.

Phloem—Phloem in the Osmundaceae is one of the easier tissues to recognize when the sieve cells occur in clusters; when the sieve cells are isolated from one another, recognition of the phloem is a difficult task. In all species of the family, sieve cells occur in V-shaped clusters with the point of the V projecting into the xylic gaps. Adjacent clusters are connected by a band of phloem one to two cells thick so that the phloem is a continuous ring completely surrounding the xylem cylinder. In any species the phloem may look as though it is discontinuous because of the small size of the cells or because crushing of the thin-walled sieve cells has occurred. Sieve cells, when recognizable as such, are generally metaphloem, the more delicate protophloem usually being obliterated by growth in stem length and maturation of the surrounding tissues. Metaphloem may also be obliterated, although not as extensively as protophloem. In fact, the process of obliteration assumes importance in characterizing sieve cells; sieve cell walls may often be sinuous from pressure resulting from the growth of the surrounding cells.

In the rhizome the protophloem occupies a position immediately inside the pericycle. Like the pericycle, the protophloem may display a vertical, diagonal or tangential orientation. In all cases observed it was a thin uniseriate layer. When the protophloem is tangentially arranged, sieve areas can be seen, further confirming its identity. In the leaf trace protophloem almost completely surrounds the xylem as a single layer.

Metaphloem can easily be distinguished from protophloem because of its larger size and position, but as isolated cells in unexpected places it may be difficult to recognize. *Osmunda cinnamomea*, for example, may have internal phloem on the adaxial side of the xylem. Criteria are therefore essential for its recognition.

Normally, the large size of sieve cells and the empty lumina are enough to identify the metaphloem (Fig. 12). Under high magnification the sieve areas represented as thin spots in the wall can be seen in transverse section. Even in perfectly transverse sections of the stem a few sieve cells will be sectioned obliquely so that sieve areas on the longitudinal walls can be seen. Often useful in con-

firmation are the so-called "globules brilliant." These are small protein granules (Janczewski, 1880) which accumulate as a thin peripheral layer near sieve areas in the walls (Fig. 13). In longitudinal section the sieve cells are quite easy to recognize because of their elongate shape, tapering and overlapping end walls and the sieve areas scattered over their surfaces (Figs. 14, 15).

One problem does exist in the classification of protophloem and metaphloem. Between the typical protophloem and metaphloem zones is a band of cells varying from one to four cells in thickness. These cells may be vertically, diagonally or tangentially oriented. When seen tangentially the cells display sieve areas similar to those of the typical metaphloem (Fig. 16). Zenetti (1895) was the first to describe these cells and gave them the name "quergestreckte Zellen." A later synonym is "porose cell." Faull (1901) considered these porose cells to be protophloem because they are tangentially continuous with the protophloem. Just as often they appear to be continuous with the metaphloem. Seward and Ford (1905) considered the porose cells to be metaphloem because they observed the porose cells differentiating after the typical protophloem.

Protophloem, by definition (Esau, 1953), "shows mature elements before the plant organ completes elongation. The metaphloem matures after this growth has taken place, although it may be differentiating during the elongation." Therefore, if the porose cells are really protophloem they would be differentiating while the rhizome was undergoing elongation. Under conditions of tangential orientation and stem elongation, it seems likely the porose cells would suffer the same fate as typical protophloem - obliteration. Moreover, the porose cells resemble metaphloem in size and pitting. Zenetti's *quergestreckte Zellen* are most likely metaphloem and they are so regarded in this study.

Leaf traces out in the cortex have metaphloem on the abaxial and adaxial sides of the xylem. The abaxial phloem is derived directly from the ring of phloem surrounding the xylic cylinder. It is supplied by the phloem from below the leaf trace. The adaxial phloem also derives from the phloem ring, but it is continuous with the phloem above the leaf trace (Fig. 17). No gaps form in the phloem because the porose cells become continuous across the xylic gaps as the trace leaves the xylem bundle.

An exception to the gapless phloem is *Osmunda cinnamomea.* Again in this respect, O. *cinnamomea* diverges from the other species of the family only at the region of forking and then not consistently. Figure 11 is at a region just below an incipient fork. It shows that the internal and external endodermal layers have become continuous through the xylic gaps, thereby approaching the true dictyostelic condition. Obviously there are also phloem gaps. Between the xylem and the internal endodermis a few sieve cells may be seen. It is this unique condition on which Faull (1901) and Jeffrey (1917) based their arguments that the modern osmundas were derived by a process of reduction from the amphiphloic siphonostelic condition.

Xylem Sheath—In the fossil representatives of the family a layer of small-celled parenchyma surrounds the xylem bundles. Zenetti (1895) reported a similar

sheath for O. *regalis*. Faull (1901) could not make out a sheath for this species. Both authors were correct. Whether or not a sheath is present depends upon the particular rhizome examined. The sheath, when present, is most strongly developed on the abaxial side of the bundle, being 5 or 6 cells thick. As it continues around the bundles and through the xylic gaps it diminishes in thickness until it is one or two cells thick or not even distinguishable on the adaxial side of the bundles. On the adaxial side the sheath becomes most noticeable when an island or bay of sheath parenchyma develops in the bundles in association with the protoxylem.

Of the species I examined, sheath development was poorest in O. *lancea*. A larger sample of this species would probably indicate an occasional well-developed sheath. *Osmunda javanica* and the other species of subgenus Plenasium consistently had a poorly-developed sheath two to three cells thick, which may be obscure or, when the cells contain tannins, pronounced. As in the rest of the family, the sheath cells in O. *javanica* are narrow and elongate, but in this species the cell walls can become thick and develop prominent circular simple pits.

X*ylem*—The most conspicuous tissue of the osmunda stem is the xylem which occurs as discrete bundles arranged in a ring. In any given transverse section the bundles may appear variously as S-shapes, U-shapes with the bay of the U pointed toward the outside or inside of the stem, O-shapes and oval-shapes. In its longitudinal course through the stem a given bundle at one time or another assumes all of these forms. The configuration of that bundle at a particular place is determined by the stage it and contiguous bundles are in during departure of the most closely associated leaf trace. Figure 10X is a diagrammatic representation of leaf trace departure in O. *regalis* for the purpose of explaining bundle shape. It could serve equally well for most other species of the family. Exceptions to these bundle shapes may occur in all species, particularly at the base of the rhizome and points of branching where the leaf trace may depart protostelically without leaving a gap.

The bundles of subgenus Plenasium display a unique shape which immediately identifies the subgenus. In a cross-section there is usually at least one bundle shaped like a question mark with the hook directed towards the outside (Fig. 10F). This unique form results because the island of parenchyma opens laterally into a leaf gap from a lower trace rather than adaxially into the pith. The arm of the hook then extends over to connect up with an oval bundle or another question mark one (Fig. 10Y) to form an inverted U-shape, which soon develops into a long horseshoe-shaped bundle. As in the rest of the family, the outer part of the horseshoe separates from the stele as a leaf trace, but the trace is unique for the family in that immediately after departure it has a pronounced C-shape (Fig. 18).

Plenasium is also unique because its traces have two protoxylem groups before the trace separates from the stem; other species have only one group. Posthumus (1924) concluded that one of the protoxylems came from each of the two bundles which fused to give rise to the leaf trace and that each bundle had its own island of parenchymna. That this does happen is indicated in Figures 19, 20, 21 of O. *javanica*. But when one of the bundles which fuses to give rise to the leaf trace is

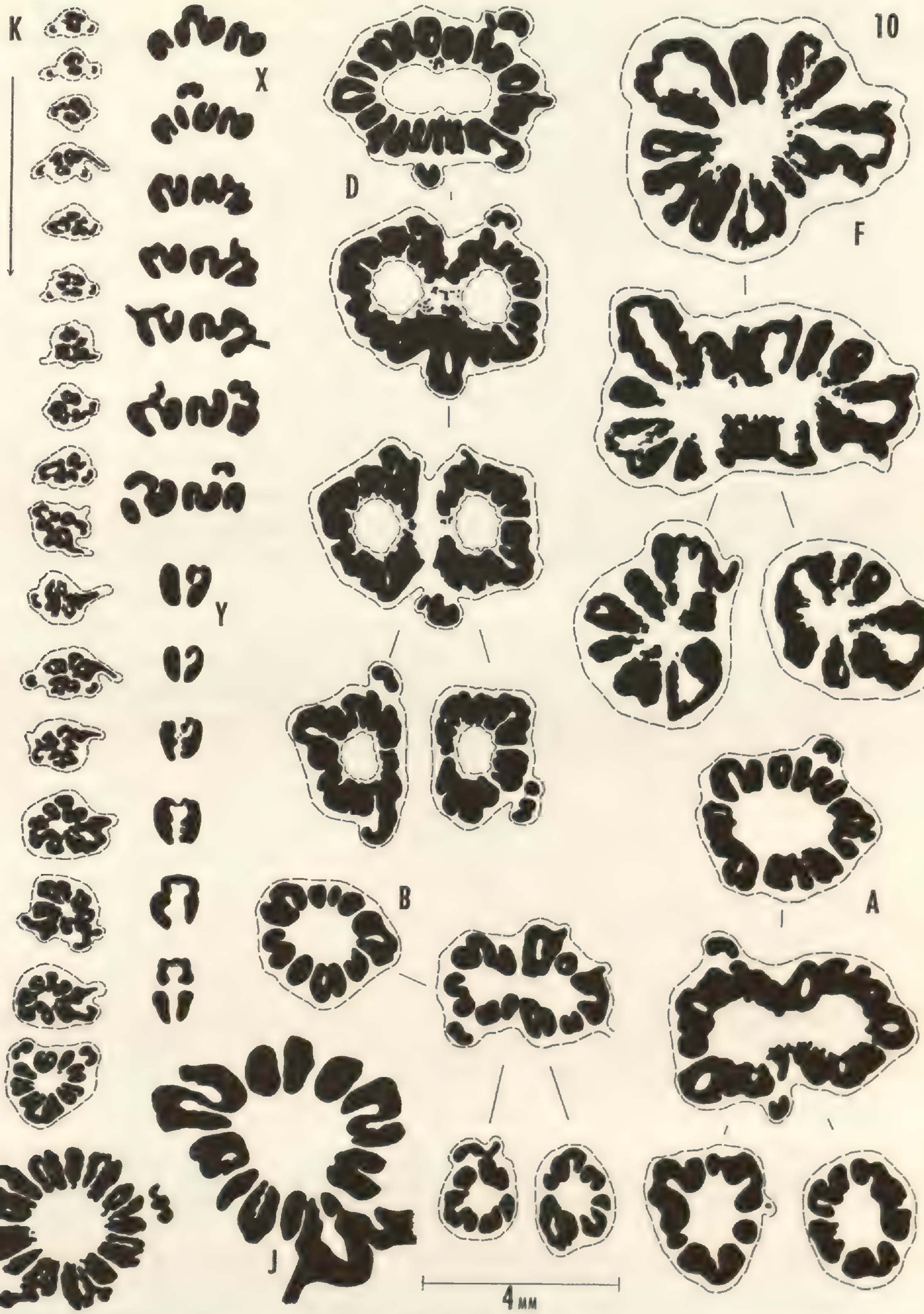


Figure 10. Xylem, black. Endodermis, broken lines. A, B. D, F. Branching of the rhizome. A. *O. regalis*, B. *O. japonica*, D. *O. cinnamomea*, F. *O. javanica*, K. *L. superba;* ontogenetic sequence from base toward apex of rhizome. J. *T. barbara;* large rhizome from Africa, X. Bundle shape in *O. regalis*, Y. Leaf trace origin in *O. javanica.*

an oval one, its protoxylem is at best obscure, if present at all. In the oval bundle a group of poorly-defined cells can usually be seen, but this group always disappears in serial sections. For *O. javanica,* then, it seems that the two protoxylem groups may always be distinct or that sometimes one protoxylem group divides to produce two groups before the trace separates from the stele. The latter of these two hypotheses seems likely because one protoxylem group does divide to produce two in *O. banksiaefolia* as is demonstrated by figures 22-25.

The number of bundles also varies from species to species. *Osmunda claytoniana* usually has the highest number (20) and *Todea* the lowest (2-6), (Faull, 1901). But there is an apparent pitfall in bundle counting. Figure 10K is a series of sections of *L. superba* from the base towards the apex of the rhizome. The other species of the family go through a similar ontogenetic sequence. At the base the rhizome is protostelic. In stages leading up to the siphonostele the bundles are often confluent with only a few gaps present. Obviously, if one were to take sections near the base he would obtain an impression quite different from the impression sections in an older part would give. My counts on bundle numbers were made as near to the apex as possible where the tissue were completely differentiated. The ranges in numbers suggest that some of my rhizomes were quite small.

For purposes of clarity, I consider two bundles to be one if they are connected by even one tracheid. Thus, someone counting the bundles in *Todea* (Fig. 10J) might say there are eleven, whereas I considered this particular stem to have ten. Counting is done in this manner because cases are encountered where it is difficult to make a decision. My numbers in the table below are therefore lower than those other people might cite.

	Number of bundles in stem X-S
O. regalis	4-11
O. *japonica*	4-11
O. *lancea*	6-8
O. *cinnamomea*	7-22
O. *claytoniana*	7-16
O. *javanicu*	3-11
O. *vachellii*	9
O. *bromeliaefolia*	3-12
O. *banksiaefolia*	4-9
T. barbara	2-7(10)
L. superba	3-11
L. hymenophylloides	5-12
L. fraseri	3-11

Branching of the rhizome is infrequent for the family but it may occur once or even twice. Age does not seem to be the determining factor as it may occur at the base of the rhizome or far removed from it. Anatomically, the first indication of branching is a flattening of the stele (Figs. 10, A,B,D,F). Bundles tend to be-

come confluent so that leaf traces may depart without leaving gaps, the most extreme case occurring in *O. lancea* (Fig. 26). This type of branching occurred in five of the species studied (*O. regalis, O. japonica, O. lancea, O. javanica* and *O. cinnamomea*), although figures 10F and 10B of *O. javanica* and *O. japonica* were drawn to indicate an alternative mode of branching where the xylem bundles do not become confluent.

The branching region of *O. cinnamomea* is the most variable of all species. In my material (Fig. 10D) the bundles make an almost continuous cylinder of wood. Faull (1901) described specimens with large ramular gaps so that the internal and external endodermis and the pith and the cortex become continuous at the branch gap. In one of my specimens the two endodermal layers came into contact through the leaf gaps (Fig. 11). Sometimes isolated tracheids or small anomalous bundles complete with endodermis are found in the pith. In one extreme example there was a nearly continuous ring of xylem with internal and external endodermis inside an outer ring of xylem with its two layers of endodermis (Fig 27).

Lang (1924) demonstrated that branching in the young sporeling of *O. regalis* is axillary, but in the mature sporophyte this relationship does not exist. The leaf traces continue to depart in a spiral manner around the branches except that on the sides where the two branches were once in contact, leaf production may be inhibited until after the two cortical layers have separated from one another. Rather than some definite relationship between branching and leaves, it appears that branching of the stem is random.

Pith—Pith in the Osmundaceae is usually composed of isodiametric or oblong parenchyma cells. A notable exception occurs in *O. javanica;* here the pith cells are elongate and are arranged in a way that suggest longitudinal files of cells (Fig. 28). In such a row, some of the cells have tapered end walls and in others they are transverse. Frequently these cells develop thick walls with large circular pits. Isolated tracheids are especially common at the periphery of the pith of *O. javanica;* followed serially, they can be seen to be derived from the bundles. Other species in which I found isolated tracheids are *O. cinnamomea* and *L. fraseri* (one cell in the center of the pith). Gwynne-Vaughan (1914) reported a "mixed pith" in *O. regalis.*

Faull (1901), in presenting his argument on the origin of the pith, makes a case of species in which sclerenchyma occurs in the pith (*O. regalis, O. cinnamomea, T. barbara*). In addition, I found sclerenchyma in *O. javanica, O. vachellii, L. fraseri* and *L. superba* (weakly developed in the latter two species).

Roots

The roots arise at the nodes and take a very erratic course in making their way out through the inner and outer cortex so that seldom is a complete root seen in a cross section of the stem (Figs. 8, 9). Rather, only parts of the roots are seen where a bend of the root has projected into the plane of sectioning. The serpentine nature of such roots appears to be derived from the resistence they meet as they grow outward, for they often go around and between the leaf bases; sometimes they

grow through the parenchymatous wings of the leaf bases but never through the sclerotic rings surrounding the traces.

Roots generally arise in pairs at the nodes from attached leaf traces; they may also leave the trace after it has separated from the stele and is out in the cortex. *Osmunda cinnamomea, Todea* and *Leptopteris* regularly have only one root associated with each trace (rarely two) while all other species of *Osmunda* usually have two roots per trace, occasionally one. Since they do not always arise at the same level, one must follow complete serial sections to be certain of how many roots are associated with each trace. Sometimes a single root arises directly from the stem xylem and bears no relation to a leaf trace. In branching regions of the rhizome, leaf traces may depart without giving rise to roots.

Always exarch, the roots most often are diarch, but occasionally they may be triarch. Kidston and Gwynne-Vaughan (1914) also noted triarch roots in *Bathypteris rhomboidea*. Seward and Ford (1903) found an occasional tetrarch root in *Todea*.

Discussion

Leaf Bases—The object of this study was to obtain criteria which could be used to identify living species of the Osmundaceae in section. It was hoped that such criteria would be useful for indicating the affinities of fossil species. Of the characters studied, only one, disposition of sclerenchyma in the leaf bases, is reliable for specific delimitation. How the species differ from one another in this respect is indicated in Figure 7. It appears unrealistic, however, to attempt to relate fossil species directly to living species. It would seem that characteristics at the generic and subgeneric levels would be more realistic and useful for phylogenetic purposes. Structure of the leaf bases is therefore summarized below for the genera and subgenera.

Subgenus Osmunda—This subgenus tends to have one long continuous sclerenchyma strand in each wing (poorly developed in *O. lancea*).

Subgenus Osmundastrum—The continuous ring that surrounds the leaf trace consists of two kinds of sclerenchyma, specialized patches of thick-walled cells and a ground tissue of thinner-walled cells.

Subgenus Plenasium—The subgenus can be characterized by sclerenchyma strands scattered within the ring.

Todea—*Todea barbara* has sclerenchyma within the ring, but lacks sclerenchyma on the adaxial side of the traces as in Plenasium.

Leptopteris—There are either a few well-developed sclerotic patches in each wing or the strands are numerous and poorly-developed.

How reliable these characteristics are is important. Where I had material of the same species from widely separated geographical areas, there was close agreement between the different samples. Kidston and Gwynne-Vaughan (1907) described the leaf bases of seven species. They do not mention the source of their material, but most likely it came from areas different from my own. The figures of species common to both studies are quite similar. Our only disagreement is the specific delimitation of *L. superba* and *L. hymenophylloides*.

Disposition of sclerenchyma in the leaf bases also seems to be an important character for delimiting fossil species and indicating their affinities. Arnold (1952) pointed out that *Osmundites spetzbergensis* and *Osmundites oregonensis* from the Eocene have the Osmundastrum type with two kinds of sclerenchyma in the ring. Kidston and Gwynne-Vaughan (1907) related *Osmundites dunlopi* and *O. dowkeri* from the Jurassic of New Zealand to the *Todea* type. Vishnu-Mittre (1955) declined to indicate whether *Osmundites sahnii* showed similarities with *Osmunda* or *Todea*. His figure of the leaf base seems to plainly indicate that this Jurassic species from India is most closely allied with *Todea*.

Cortex—In Osmunda the boundaries between the inner and outer cortex and the mantel of leaf bases are usually well-defined. The sclerotic ring of the leaf trace is not noticeable until it protrudes from the outer edge of the cortex. In *Todea* and *Leptopteris* the cortical boundaries are generally not as well defined and the sclerotic ring is apparent where the leaf trace is within the cortex. However, one cannot always depend on these characters to recognize *Todea* and *Leptopteris* because the cortex of these genera may at times look quite like that of *Osmunda*. Figures in the literature seem to indicate that cortical characters are not too important for the fossils.

The number of leaf traces in the cortex, however, might well be important for delimiting fossil species and their affinities. Subgenus Osmunda, *Todea* and *Leptopteris* are rather similar in having up to 15 traces in the cortex. Osmundastrum typically has the highest number for the family (11-27), while Plenasium usually has the lowest (3-8). The point along the length of the rhizome at which the section is taken is important. In a particular rhizome of *L. superba* 11 cm long, sections were taken about every 1.5 cm. From the base to the apex the following progression in number of cortical leaf traces was observed: 3, 5, 5, 9, 13, 16, 22. This increase in number of stem traces correlates with an increasing fraction of phyllotaxy and an increasing stem size.

The low number of traces in the cortex of subgenus Plenasium, however, is real and not a result of working with immature material. Two of the rhizomes of *O. javanica* from Ceylon were the largest rhizomes of all the species I had. Both were about 15 inches long. The highest number of traces observed for this species was six in the outer cortex and one in the inner cortex. This low number of traces is related to the broad angle of leaf trace departure (30-45°).

Number of Stem Bundles—The number of stem bundles of the subgenera and genera may be summarized as follows: subgenus Osmunda, 4-11; Osmundastrum, 7-22; Plenasium, 3-12; Todea, 2-7(10); Leptopteris, 3-12.

The number of bundles in *Todea* and *Leptopteris* has long been considered to be relatively low because of the shortness of the xylic gaps and the subsequent confluence of the bundles (Seward and Ford, 1903). For the most part I have to agree with this generalization, but two rhizomes are suggestive of an opposite viewpoint. One rhizome of *Todea barbara* from Africa about 15 cm long and one rhizome of *L. superba* about 11 cm long do not agree with this generalization. Figure 10J (compare with Fig. 9J) is of *T. barbara*. It has 10 bundles and no

indication of the bundle confluence which is supposedly typical of *Todea*. *Leptopteris superba* (Fig. 10K) similarly departs from the typical *Leptopteris* image perpetuated in the literature. These two rhizomes, which were larger than any of my other material for the two genera are by no means large when compared to Seward and Ford's one ton *Todea* and Compton's (1922) ten foot *L. wilkesiana*. They seem to indicate that as the rhizome increases in size, *Todea* and *Leptopteris* begin to look more like *Osmunda* in terms of bundle numbers.

Apparently the reason for the persistent *Todea-Leptopteris* generalization is the difficulty for most botanists of obtaining adequate material. Thus, if one receives a large living rhizome, he might be reluctant to destroy it for purposes of sectioning. It might prove interesting, though, if a large rhizome of *Todea* or *Leptopteris* were sacrificed. Moreover, it might prove to be important evolutionarily. *Osmundites sahnii* from the Jurassic of India has about 20 bundles (by my method of counting from Vishnu-Mittre's figure, 1955). The sclerenchyma in its leaf bases is quite similar to that of *T. barbara*. In spite of the similarity in the leaf bases, one would be reluctant to align such a fossil with *Todea* if *Todea* were thought to have only 2-6 confluent bundles.

Branching—Fossil representatives of the Osmundaceae such as *Zalesskya* and *Osmundites dunlopi* had continuous cylinders of wood with few or no xylic gaps. These are used as evidence for intermediate stages in the evolution of the osmundaceous stele from the protostelic to the siphonostelic condition. The work of Kidston and Gwynne-Vaughan (1906-14) has documented this hypothesis so well that most botanists would accept it today. Occasionally fossils have turned up since their time to substantiate their views. Zalessky (1931) described a new genus, *Petcheropteris*, with a continuous cylinder of xylem. Since the stele was oval (9 x 6.5 mm), Zalessky concluded that it had been flattened in preservation.

Most likely he was correct, but an alternative view might be that the section was made at a branching region. Figures 10 A,B,D,F and 26 indicate that the stele of the living species becomes flattened in the branching region; the xylem also tends to become continuous (Fig. 26). A section through a branching region of a fossil, then, might conceal a cylinder interrupted by xylic gaps below the branch. Considering the age of *Petcheropteris* (Permian), this interpretation hardly seems to apply because the siphonostele was not established until the Jurassic, but it would be a factor to consider in more recent fossils.

Pith—The pith and its origin have long been the center of arguments in the Osmundaceae. Faull (1901) believed that the pith arose from cortical tissue penetrating the ramular gaps. His argument was highly theoretical, however, with very little evidence to support it. The intrastelar origin of the pith suggested by Kidston and Gwynne-Vaughan (1907-1914), is much better documented by the fossil record. *Thamnopteris* was protostelic with a transition from long, slender tracheids toward the outside of the xylem to short, stout tracheids toward the inside. *Zalesskya* may or may not have had a pith but had a continuous cylinder of xylem, again showing a gradation in tracheid size toward the center of the xylem. The genus *Chasmatopteris* of Zalessky (1931) shows the origin of xylic gaps which penetrated only

the outer zone of slender tracheids. *Osmundites kolbei* had a mixed pith. Daugherty (1960) described *Itopsidema* which had a few tracheids in the pith, although he concluded it could not in any sense be construed as a mixed pith. *Osmundites dunlopi* had a nearly continuous ring of xylem with few or no xylic gaps. Later fossil species have the typical xylic gaps of the living osmundas. Faull's argument, on the other hand is only supported by *O. cinnamomea; Osmundites skidegatensis,* which had true leaf gaps and internal phloem; and *Osmundites carnieri,* with the external and internal endodermal layers connected to form meristeles.

Evidence in support of the intrastelar origin from living material comes from *L. superba* and *L. hymenophylloides* (Seward and Ford, 1903) which sometimes have large, stout tracheids bordering the pith. In this study, the elongate pith cells which sometimes occur in longitudinal rows of 3 or 4 cells in *O. javanica* are viewed as evidence for the intrastelar theory. The cells terminating these files of cells often have tapered end walls while the middle cells have transverse end walls. Daugherty (1960) described the same condition in *Itopsidema* and considered the rows of cells to be an indication that the pith arose by cross-septation of elongate procambial elements which failed to develop into tracheids.

Isolated tracheids are especially common in the pith of *O. javanica.* Posthumus (1924) interpreted these tracheids as vestiges of the protostelic condition in the past history of the family. To me, the longitudinal seriation of pith cells is a better indication of an historical protostele because the tracheids are always near the bundles and when followed serially they can be observed to be derived from bundles in the process of giving off leaf traces. That is, these isolated tracheids are ontogenetically part of the xylem bundles and not part of the pith.

Most people today would probably consider the pith to be intrastelar in origin. It does not seem likely that further descriptive work will ever resolve the problem of pith origin to everyone's satisfaction. A more profitable line of research will probably be experimental. Clutter and Sussex (1951), for example, have induced the development of tracheary elements in the pith of *Nicotiana* by treatment with auxin. Steeves and Briggs (1960) demonstrated that auxin promotes tracheid differentiation in the leaf trace of *O. cinnamomea.* Wardlow (1946) produced a "mixed pith" in *O. regalis* and *T. barbara* by destroying newly-formed leaf primordia as soon as they developed.

Plenasium: Leaf Trace Origin—The deep C-shaped trace with two protoxylem groups while the trace is still attached to the stele is unique to the subgenus Plenasium. The two protoxylem groups may originate from a single group which divides or they may be decurrent from the leaf trace into the bundles of the stem as two distinct groups along their entire course, each associated with its own island of parenchyma.

No other osmundaceous plant regularly exhibits this pattern. Indeed, the only other plant even remotely related to the Osmundaceae which had two protoxylems in the attached leaf trace was the zygopterid genus *Asterochlaenopsis* (Sahni, 1930). Its star-shaped stele with radiating arms of xylem, at the tips of which several leaf traces and roots arise, would seem to remove it from any zygopterid line which might have given rise to the Osmundaceae.

Since two protoxylem groups are found nowhere else in the history of the Osmundaceae, it must be concluded that it is a derived feature. It seems likely that the type where the two groups are always distinct arose through the type where a single strand divides to produce two. Interesting is the fact that two protoxylem groups occasionally were observed in the leaf traces of *O. regalis* from India. Further, the leaf base sclerenchyma of *O. regalis* and *O. javanica* (Figs. 7, A,F) is rather similar; both have sclerenchyma within the ring. The only difference is that the sclerenchyma in the wings of *O. regalis* occurs as continuous strips, while in *O. javanica* it occurs as scattered strands. If the two protoxylems of the Plenasium leaf trace are to be related to the other Osmundaceae, then, subgenus Osmunda would seem to be the only logical place.

Correlation of Anatomical Variation with Geographical Distribution—For each of four species—*O. regalis, O. cinnamomea, O. javanica* and *T. barbara*—I had material from widely separated localities. *Osmunda regalis* was sent to me from New England and Mississippi in the United States and from India. *Osmunda cinnamomea* came from New England, Mississippi and Thailand. *Osmunda javanica* was collected in Ceylon and Thailand. From New Zealand and South Africa I obtained rhizomes of *T. barbara.*

I could detect no significant variation in rhizomes of *O. regalis* from the United States. However, *O. regalis* from India (Mahabaleshwar, about 75 miles southeast of Poona) differed from the above material in the manner of its leaf trace origin. Usually there was only one protoxylem point associated with each trace; occasionally there were two protoxylem groups in the leaf trace before it departed from the stele. Two protoxylem groups per leaf trace is a character regularly associated with Plenasium. *Osmunda javanica,* of the subgenus Plenasium, is found in Ceylon, perhaps close enough to India for a transition between the two species to occur. More material from the Mahabaleshwar locality should be examined to check this point.

Osmunda cinnamomea within the United States was quite variable. In a specimen from Mississippi, patches of tracheids occurred within the pith and the internal endodermis was lacking; in a specimen from Massachusetts, a complete cylinder of xylem was found within the normal ring of xylem bundles. I do not believe these differences can be credited to geographical variation; rather, they are probably peculiarities of the particular rhizomes. The likelihood of this explanation is increased because the above variations were observed at branching regions; Faull's work (1901) on 25 forks points out how inconsistent this region is. The material from Thailand displayed no great differences except for a much smaller size.

A good character for the recognition of the subgenus Plenasium is the deep C-shape of the leaf trace as soon as it departs from the stele. The specimen of *O. javanica* I received from Thailand carried this tendency to an extreme. The trace was almost completely closed; only a few crushed phloem cells interrupted the arms of the trace. While all the leaf traces of this particular rhizome had exaggerated traces, only a few exhibited the tendency to this degree. The apparent

extreme closing of these traces may partly be accounted for by the obliqueness of the sections.

Todea barbara from South Africa most noticeably differed from New Zealand material in its larger size and higher number of stem bundles (10). Confluence of the xylem strands was also less marked in the African material and sclerenchyma in the pith was absent. In this case, the difference in size is considered to be important for the particular specimen studied, but not for the geographical separation.

An obvious limitation in these geographical comparisons and for the whole study is the small sizes of my samples. It is therefore difficult to know whether it was really geographical variation or simply individual variation which has been considered. For the most part, rhizomes appeared to be consistent from wherever they came. Variations such as tracheids in the pith, anomalous bundles in the pith or slight differences in trace shape appear to be variations peculiar to the particular rhizomes studied. Such variations might easily be considered important enough to delimit fossil genera. One should be cautious of such characters, however, especially if sections are made at apparent branching regions. An occasional leaf trace with two protoxylems in *O. regalis* from India may or may not be important. I am inclined to consider it important because it occurred in both of my rhizomes from this locality. More material should be examined, however, to be certain of its constancy.

Taxonomic Suggestions—Two species of Osmunda probably should be reduced to synonymy or treated as varieties. *Osmunda japonica* has been variously treated as a species or as a variety of *O. regalis*. Its key character as a species is the disposition of its fertile pinnae; sometimes the fronds are completely dimorphic, sometimes incompletely dimorphic. Indications are that the position of the fertile pinnae is relatively plastic for *Osmunda*. Chrysler (1926), for example, reported a specimen of *O. regalis* from the United States which was completely dimorphic. Hooker and Baker (1883) found the same degree of dimorphism in specimens from Natal. While these are just two cases of complete dimorphism for *O. regalis*, they do point out that the phenomenon can occur and in places other than Japan. If the criterion of dimorphism is eliminated from species consideration, *O. japonica* differs from *O. regalis* in having larger pinnules with a more acuminate apex. Arrangement of the sclerenchyma in the leaf bases is not the same, but the difference is slight (Figs. 7, A,B). In rhizome anatomy I could find no difference at all.

Posthumus (1924) considered *O. vachellii* and *O. javanica* to be one species, *O. javanica*, and I would agree with him. *Osmunda javanica* bears its fertile pinnae about in the middle of the rachis with sterile pinnae on either side; margins of the pinnae may be entire or toothed. The key characters for *O. vachellii* are the always basal fertile pinnae and the always entire vegetative pinnae. I have seen only two specimens of *O. vachellii*, but if the position of the fertile pinnae is as variable in this species as it is in *O. japonica*, then it probably does not merit the rank of species. Further, I cannot distinguish *O. javanica* and *O. vachellii* anatomically.

Presl (1845) segregated *Leptopteris* from *Todea* on the basis of the filmy habit

in the former genus; *Todea* is coriaceous. Another difference is the densely packed sporangia on the abaxial pinnae surfaces of *Todea* while in *Leptopteris* the sporangia are few. Position of the annulus also differs. In position and number of cells in the annulus, Osmunda appears to be closer to *Leptopteris* than *Todea* does. Most authors since Presl, however, consider *Leptopteris* to be a part of the genus *Todea.*

Anatomically, it is difficult to distinguish the two genera except by the leaf bases. *Todea* has sclerenchyma scattered within the ring, a feature that is absent in *Leptopteris.* The two genera may have sclerenchyma in the pith, although it is only a weak development in *Leptopteris* and it is not a constant feature of *Todea.* Both genera share a similar ontogenetic stem sequence and display a low bundle number because of the confluence between the bundles. Anatomy, then, does not provide conclusive evidence for either retaining or combining the two genera.

Such a decision must be based on the gross morphology of the fronds. Generally the filmy habit is interpreted as a derived condition which develops in association with a moist habitat. *Todea* and *Leptopteris* overlap in distribution under humid conditions in eastern Australia and New Zealand. Since inclusion of the filmy habit and coriaceous habit in one genus does not make an unnatural assemblage, I favor recognition of *Todea* only. Precedent for such action may be seen in the genera *Asplenium* and *Adiantum,* both of which include filmy and herbaceous species. The filmy habit is functional for identification purposes, however, so that two sections of *Todea* would be useful. Allen (1961) treated the species in New Zealand in this way.

Summary and Conclusions

Thirteen species of the Osmundaceae were compared in the following respects: gross morphology of the fronds, epidermal structure, sporangial structure, leaf base anatomy and rhizome morphology. Morphological and anatomical observations support the naturalness of three subgenera in the genus *Osmunda* and suggest that *Leptopteris* could be included within the genus *Todea.*

Of the anatomical characters studied, only one, that of sclerenchyma disposition in the leaf bases, appears to be reliable enough to characterize species, subgenera and genera. It is the best character for delimiting fossil as well as living species anatomically so that it should be included in the description of any new species or in any future monographic work. This observation appears to reiterate an already-known fact, that the Osmundaceae are quite consistent in their anatomical structure and have been so for a long period of time.

Structures in the family which have apparently been most plastic are the fronds. Disposition of the fertile pinnae is a character relied on for delimiting species in the genus *Osmunda.* However, a great deal of variation exists in the positioning of fertile pinnae in *O. regalis, O. claytoniana* and *O. javanica.* This variation suggests that a rigid delimitation of fertile pinnae position for a species is not realistic; rather, a range of positions better approximates the conditions found. Based on this evidence, I believe that *O. japonica* would be best treated as a variety of *O. regalis* and that *O. vachellii* should be reduced to synonymy with *O. javanica.* No anatomical details which I observed justify their being ranked as separate species.

Sporangial characters are not significant for recognizing species in the family. They may be used with some reservations for the genera and subgenera. The most objective character is the distance of the annulus from the sporangium stalk. The annulus of *Leptopteris* touches the stalk or is close to it; that of *Todea* is farthest removed from the stalk and that of *Osmunda* occupies a position intermediate between these extremes.

Stomatal structure is general for *Osmunda* and *Todea* and cannot be used for specific identification; *Leptopteris* lacks stomata.

The cortex of *Osmunda* is homogeneous in its cell types so that the sclerotic ring of the leaf trace is not apparent within the cortex; in *Todea* and *Leptopteris* the sclerotic ring may often be seen in the cortex because of its thicker-walled cells with small lumina. Osmundastrum typically has the highest number of leaf traces in the cortex (11-27); Plenasium has the lowest number (3-8) and the traces are an exaggerated C-shape as soon as they leave the stele. Even while attached to the stele the traces of Plenasium are unique because they have two protoxylem groups.

The number of bundles in the stem has always received attention, particularly in the fossil representatives of the family. Generally the fossil representatives had a high bundle number (40-50); the relatively low numbers in living species indicate a trend for reduction in bundle numbers. Subgenus Osmundastrum approaches the fossil condition most closely with up to 22 bundles; subgenus Osmunda has about 15; Plenasium is the lowest for the genus Osmunda with about 9. *Todea* and *Leptopteris* have been characterized in the past by a low bundle number (2-7) and confluence of bundles was considered to be diagnostic. Two relatively large rhizomes of *L. superba* and *T. barbara* suggest that as stem size increases these two genera lose the character of confluent strands and bundle number increases. Since the two genera may assume massive proportions, larger stems may possibly approach in character the large fossil stems found in the areas where *Todea* and *Leptopteris* grow today.

The pith of *O. javanica* adds further support to the concept of an intrastelar origin for the pith. Isolated tracheids may occur near the periphery of the pith and the parenchyma cells are elongate and arranged in rows which suggest derivation from procambial cells that underwent cross-septation and failed to develop typical tracheidal wall sculpturing.

Branching of the rhizome is infrequent. The point at which a rhizome does branch may differ from the unbranched region in anatomical structure. Generally, in branching zones the bundles tend to become confluent and leaf traces may depart from the stele without leaving gaps. A fossil sectioned at such a region could easily lead to unwarranted conclusions about the nature of the stele. *Osmunda cinnamomea* is quite variable at forking regions of the stem. Such features as isolated tracheids and anomalous bundles in the pith occur at this zone. I would attach no great significance to them and consider them to be oddities of the particular rhizome, although such variation seems to be typical of *O. cinnamomea.*

Geographical variation for what material I had does not seem to be significant.

Polunin (1960) mentioned six varieties of *O. regalis* and their distribution. I had only two of his varieties, which came from the United States and Japan. These exhibited only a slight difference in the sclerenchyma of the leaf bases. Comparison with the other varieties might be important for determining the constancy of the sclerenchyma and might give some idea about speciation.

Serious limitations of this work are the small sample sizes and the small specimen sizes. The cost of shipping materials over great distances precluded working on large specimens in great numbers. For similar reasons I was unable to obtain material of *L. wilkesiana* from New Caledonia, *L. moorei* from Lord Howe Island and *L. alpina* from New Guinea. This outcome was unfortunate because my impression is that larger rhizomes of *Todea* and *Leptopteris* would be strikingly different from the smaller ones and more like fossil species. Since there is an abrupt change between the fossil species with high bundle numbers and living species (as we know them) with low bundle numbers, larger rhizomes of *Todea* should be checked, for this species might be transitional between the two extremes.

One thing apparent from this study is that evolution proceeded most rapidly in the Osmundaceae during its early history in the Permian and Jurassic periods. Rhizome morphology since this time has been quite constant. Leaf base anatomy already resembled modern types by the Jurassic. The structure apparently most subject to evolutionary change is the frond. It is therefore the best structure for delimiting modern species. But it, too, is evolutionarily conservative, for *Todites Williamsoni*, quite similar to *Todea barbara*, had evolved by Jurassic times and was almost cosmopolitan in its distribution. Nevertheless, in spite of the slow rates of evolution of the family, further investigation on *T. barbara*, *Leptopteris* and southeast Asian species of *Osmunda* may help to indicate evolutionary pathways for reduction of stem size, reduction in bundle number and development of the leaf trace with two protoxylems.

Acknowledgments

I would like to recognize the many contributors to this study who sent materials to me from different parts of the world. Without their help, the problem could not have been undertaken.

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Explanation of Plate

Plate 1

Figure 11. *O. cinnamomea* (X-S) branching region with internal (ie) external endodermis (ee) continuous through a leaf gap.

Figure 12. *O. japonica* (X-S) depicting protophloem (pp) and metaphloem (mp) in stem.

Figure 13. *O. regalis* (X-S) with "globules brilliants" apparent periphery of sieve cell walls.

Figure 14. *O. cinnamomea* (L-S) indicating sieve areas on sieve cells.

Figure 15. *O. cinnamomea* (L-S) the sieve cells of fig. 14 at higher magnification showing details of sieve area in section.

Figure 16. *O. claytoniana* (X-S) with porose cells (pc) tangentially oriented in phloem of stem.

Figure 17. *O. claytoniana* (L-S) showing origin of abaxial and adaxial metaphloem (p, p) in leaf trace.

Figure 18. *O. banksiaefolia* (X-S showing the pronounced C-shape of the Plenasium leaf trace immediately after separation from the stele.

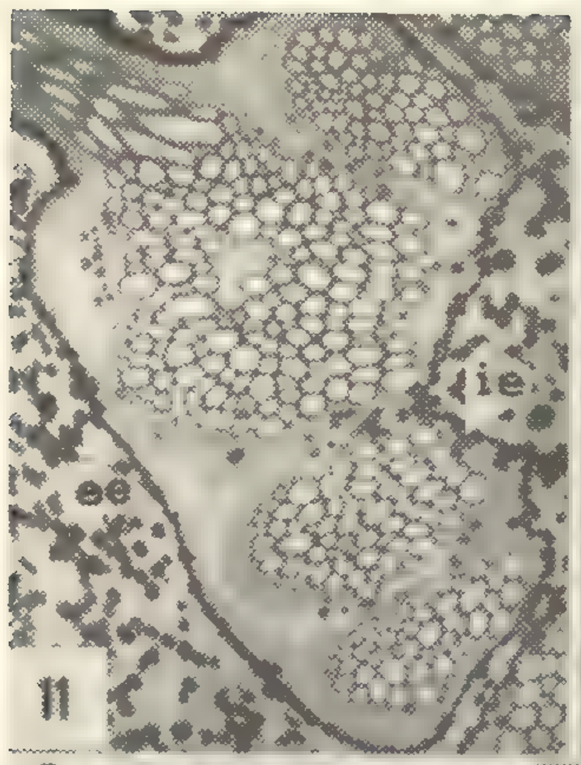
Figures 19-21. Examples of departures of leaf traces with two distinct protoxylem groups (px). Fig. 19. *O. bromeliaefolia*. Figs. 20, 21. *O. javanica*.

Figures 18, 22, 23, 24, 25. *O. banksiaefolia* (X-S), showing departure of leaf trace with one protoxylem group (px) giving rise to two groups.

Figure 26. *O. lancea* (X-S) showing a nearly continuous xylem ring in a branching region; inner cortex, endodermis, pericycle, phloem and pith had been decayed away in this specimen.

Figure 27. *O. cinnamomea* (X-S) branching region with an internal cylinder of xylem joined at several points with external xylem.

Figure 28. *O. javanica* (L-S) showing pith with elongate cells arranged in longitudinal series.



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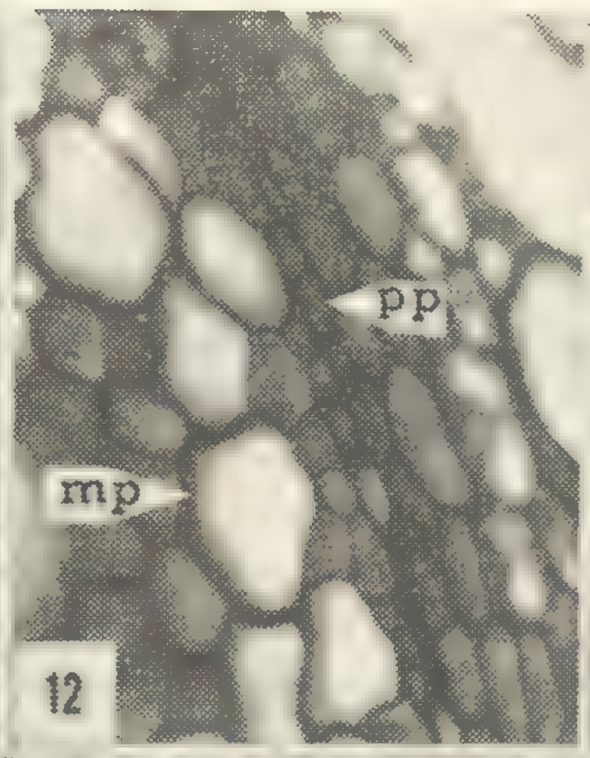

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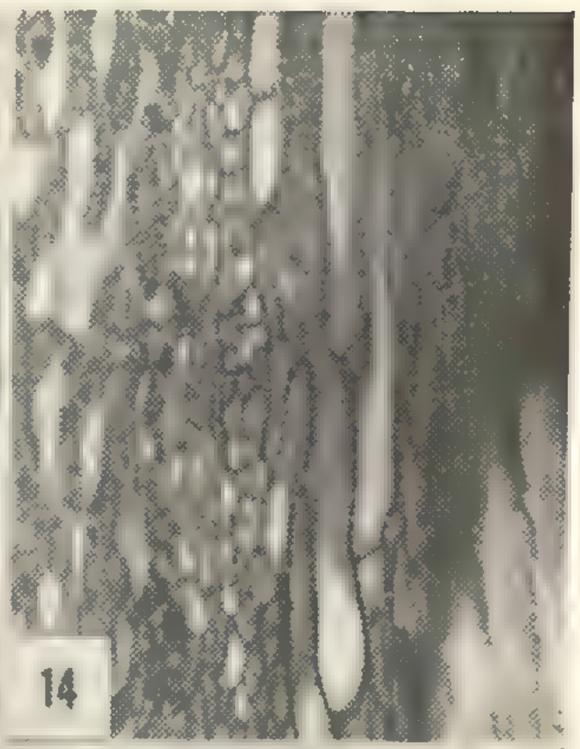

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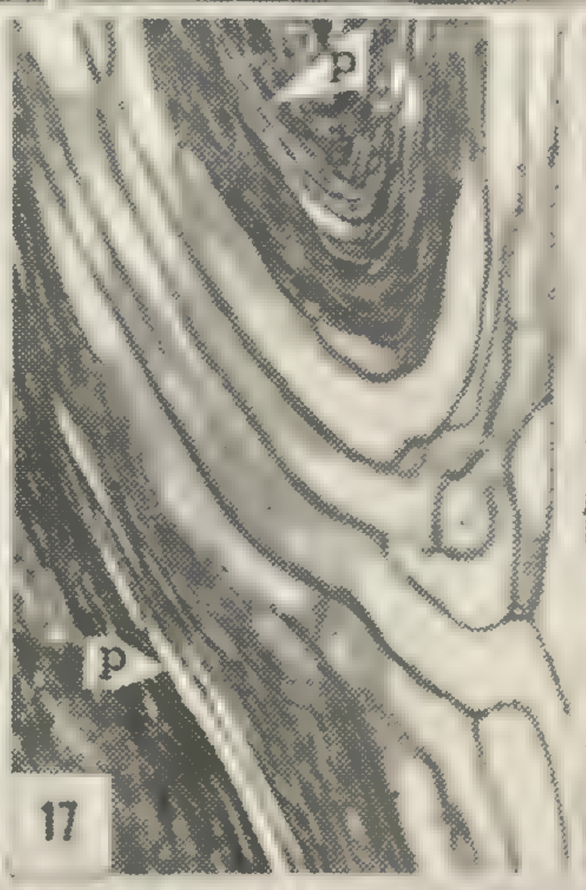

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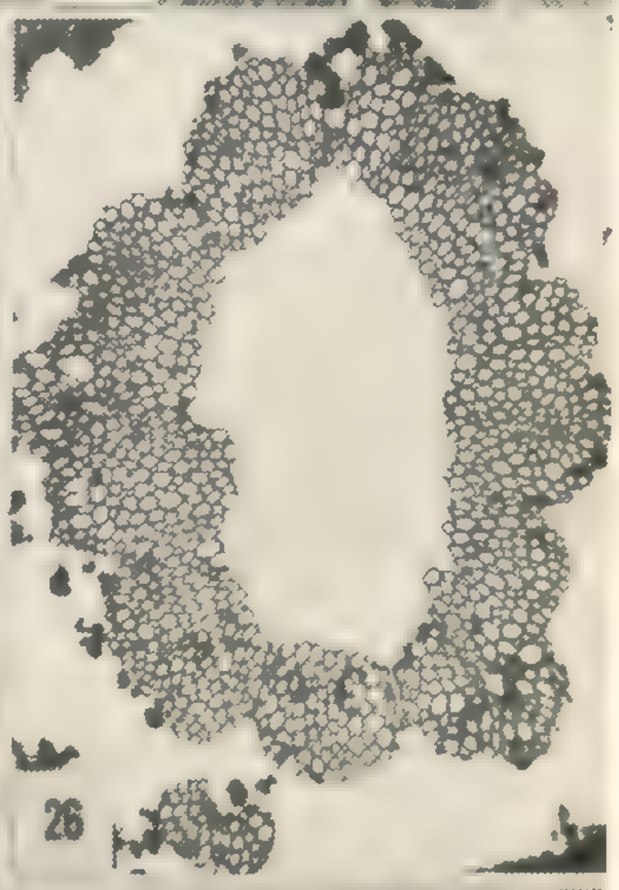

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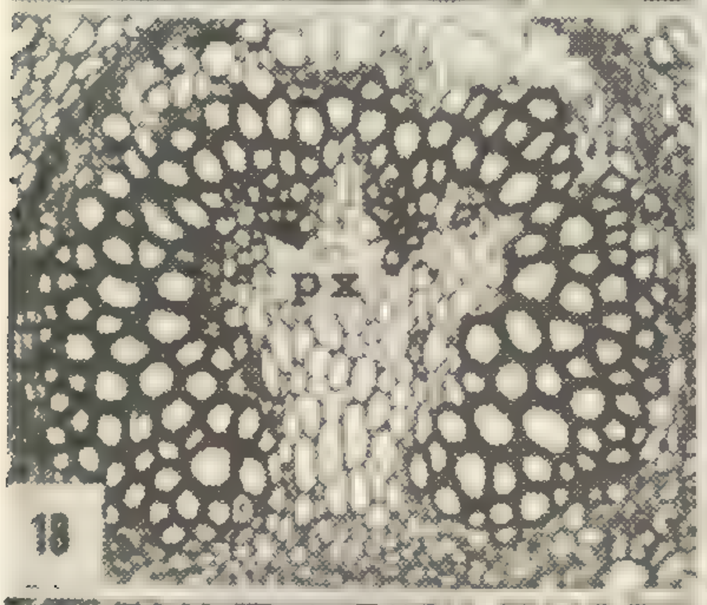

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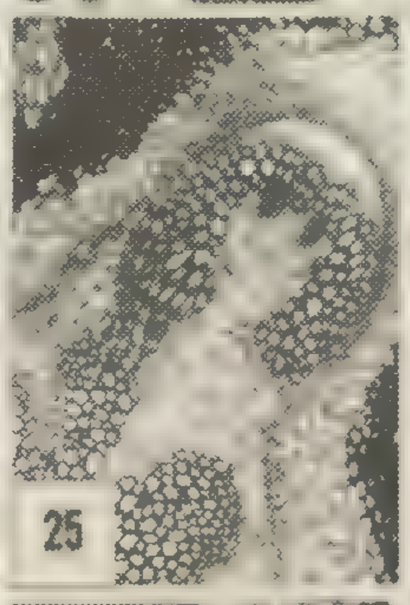

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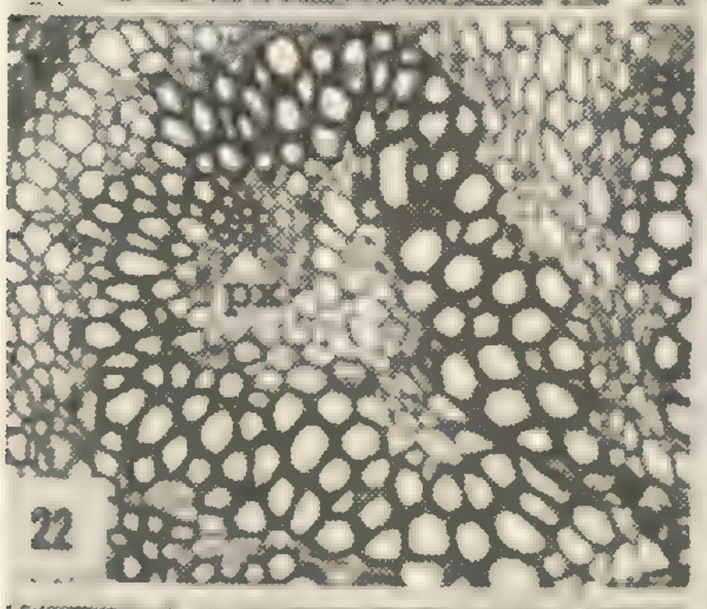

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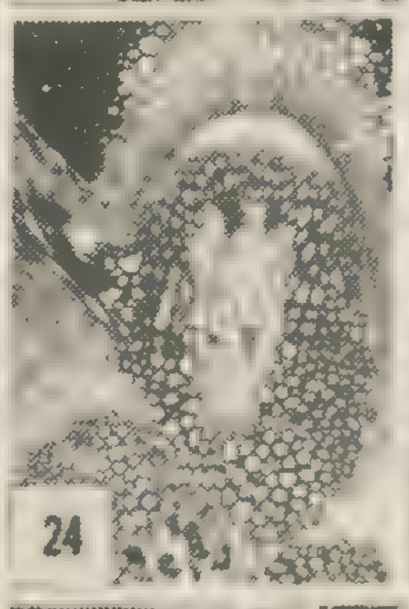

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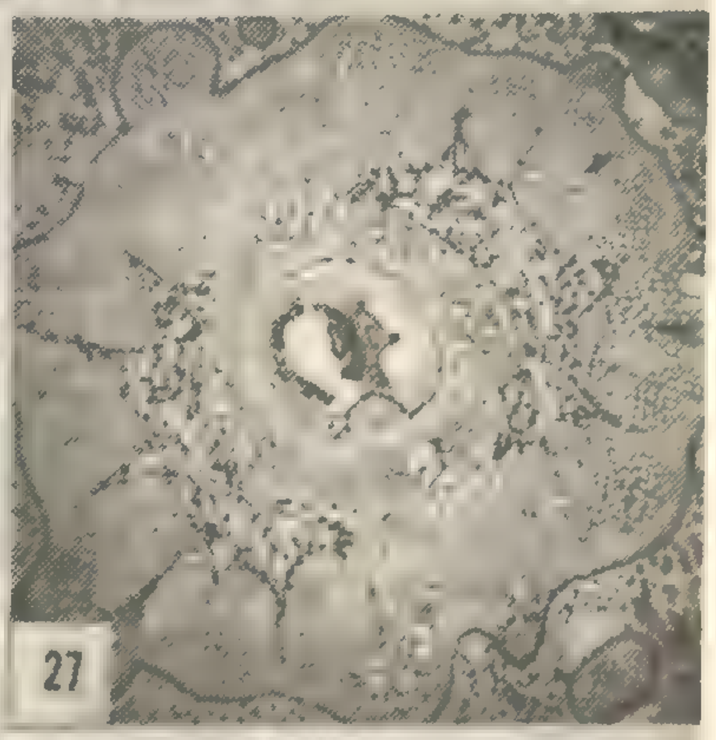

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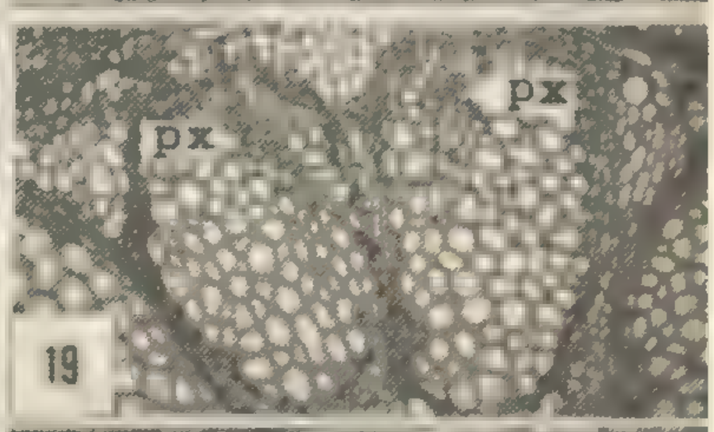

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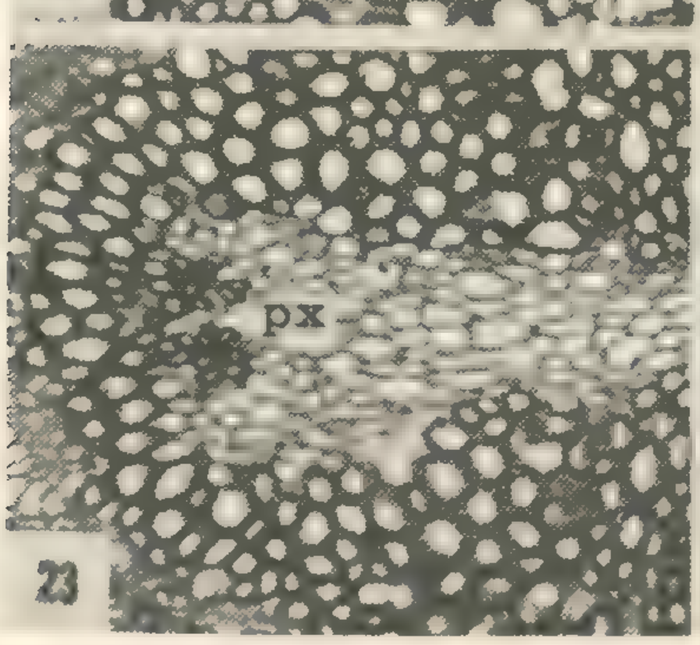

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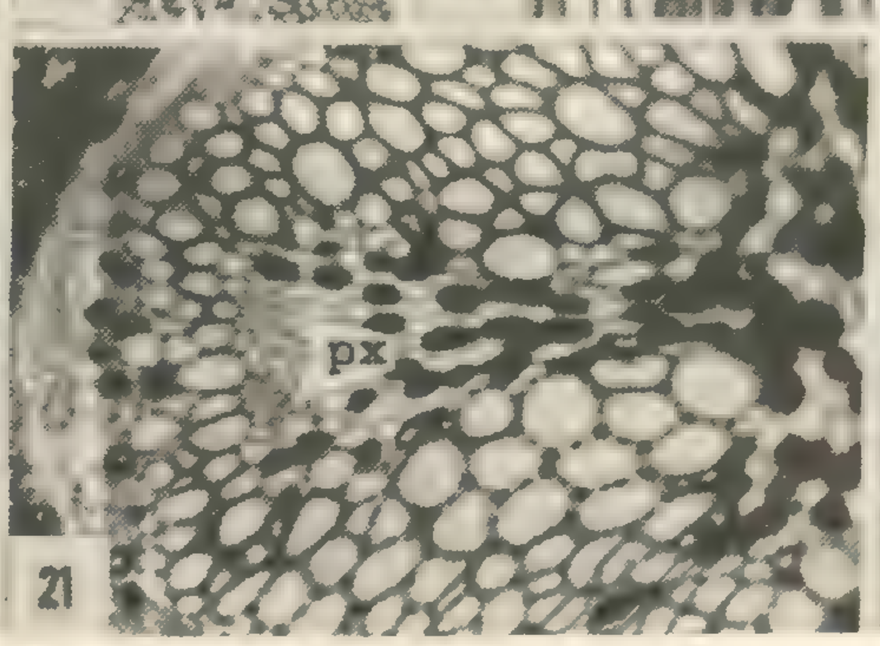

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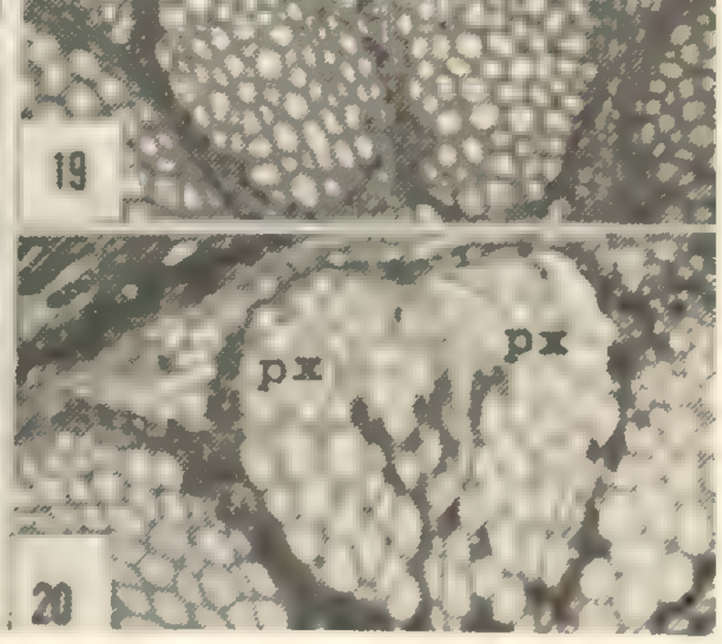

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THE FLORAL MORPHOLOGY OF SECAMONE AND THE EVOLUTION OF THE POLLINATING APPARATUS IN ASCLEPIADACEAE*

FUAD M. SAFWAT

Abstract

The floral anatomy and morphology of several species of *Secamone* is discussed. Ontogenetic studies reveal that the anthers are 4-locular. In this respect *Secamone* differs from other members of the subfamily Cynanchoideae of Asclepiadaceae. The bilocular anthers of other Cynanchoideae are a result of phylogenetic suppression of the two outer locules of each anther, as shown by ontogenetic studies and by the origin and nature of the tapetal tissue. Ontogeny of the pollinum sacs is followed in *Secamone*. Pollen mother cells undergo considerable elongation before the formation of the tetrads. The two meiotic divisions are simultaneous, contrasting in this respect with the successive divisions of other Cynanchoideae and agreeing with the Periplocoideae and Apocynaceae. The resulting tetrads have different configurations depending on the direction of the second meiotic spindle; they are rhomboidal or T-shaped. This is in sharp contrast to the linear tetrads characteristic of all other members of Cynanchoideae, but similar to Periplocoideae and Apocynaceae. The ontogeny of the stigma head is followed, which reveals that at maturity the entire stigma head of *Secamone* is glandular, contrasting sharply with the five restricted glandular regions of this structure in other Asclepiadaceae and agreeing with similar structures of the Apocynaceae. The five glandular furrows of *Secamone* in which the simple translators are secreted are not well defined. Each translator consists of a more or less solid portion which is pushed upward and slightly outward by another more or less fluid substance. Thus the whole translator of *Secamone* is comparable to the stalk-adhesive disc of Periplocoideae and the corpusculum of higher Cynanchoideae. *Secamone* thus presents several primitive characters shared with Periplocoideae and Apocynaceae but not with other Cynanchoideae (where it has been placed by taxonomists). It shares with other Cynanchoideae, however, the presence of pollinium sacs and a primitive development of the translators. It is difficult to draw a sharp line between members of Apocynaceae and Aslepiadaceae since they apparently represent closely consecutive levels of floral evolution.

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Introduction

One of the most significant families of flowering plants from the evolutionary point of view is the Asclepiadaceae. The interest of this group is derived from the floral structure of its members, which exhibit extreme adaptation to insect pollination.

As early as 1809, Robert Brown separated the Asclepiadaceae from the Apocynaceae. The basis for both the separation of the families and the currently accepted subdivision of subfamilies within them has been designed to reflect increasing adaptation to entomophily. The Apocynaceae, generally speaking, have pollinating habits scarcely more elaborate than those of the average entomophilous angiosperm; the Asclepiadaceae, on the other hand, are distinguished by cross-pollinating devises equalled in complexity only by the orchids. But impressive intergradation is apparent among the two constitutent subfamilies of each.

According to Schumann (1895) the Apocynaceae are divisible into two subfamilies: (1) the Plumerioideae, in which the stamens are free or loosely gathered around the "stigma head," the anthers with a small connective and the four anther

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* Part of an investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

sacs full of pollen, which is granular (tetradinous in *Condylocarpon*), with no translating apparatus developed; (2) the Echitoideae (or Apocynoideae), in which the stamens are connivent about the stigma head, with a greatly enlarged connective and four anther locules empty at the base and with granular pollen (except in a few genera, as *Apocynum*, where the pollen grains remain in tetrads). In some genera of the latter subfamily a primitive pollen-translating apparatus is developed through agglutination of excess secretions of the stigma head.

Similarly, the Asclepiadaceae are divided into two subfamilies: (1) the Periplocoideae, in which the anthers are connivent with the stigma head, with four locules full of pollen which remains in tetrads, and a rather elaborate pollinating translator apparatus in many genera; (2) the Cynanchoideae (or Asclepioideae), in which the stamens usually are adnate to the stigma head, each anther lobe having but one pollinium sac completely enclosing the pollen (two sacs in the tribe Secamoneae), and the pollinating apparatus is most highly specialized. In Periplocoideae a translator consists usually of an open shovel- or cornucopia-like receptacle to receive pollen tetrads shed at maturity and a lower stalk-adhesive disc combination which becomes glued to the body of the pollinator; in Cynanchoideae the translator is a yoke-like structure consisting of a solid body, the corpusculum or "gland," and two lateral cartilaginous straps, the translator arms, to which the pollinium sacs become glued at maturity—the corpusculum bears a longitudinal fissure upon its outer face, within which the pollinating insect's appendage becomes clamped mechanically.

Although over 300 genera have been described in this family, morphological and anatomical studies have been restricted to a very small number of them, notably *Asclepias*. The floral structure of the African and Asian asclepiads has scarcely been touched from this standpoint although those two great continents are centers of the most primitive genera of the family. It is almost axiomatic that the primitive groups within a given family may furnish more evolutionary information than the more advanced ones.

Secamone, of the subfamily Cynanchoideae, is one of many neglected genera of Asclepiadaceae which await extensive morphological and anatomical investigation, and which further merits attention since it is one of the few genera of the family indigenous to both Asia and Africa. Species of *Secamone* are twining or prostrate, frequently branched shrubs or undershrubs with leathery or herbaceous, often small leaves. The terminal or lateral inflorescences are cymes or panicles with white or yellowish flowers. The flowers are very minute and in describing them R. Brown wrote

> "From the extreme minuteness of the parts, no genus has been more difficult to determine than this . . . . . ."

One of the problems which faced earlier asclepiad morphologists concerned the number of anther locules in this genus, in which the pollinium bears paired, instead of the customary solitary, pollen sacs at either end of the translator. In describing this situation authors almost always have stated merely that the complimentary pairs of pollinia "adhere closely at maturity." When it is recalled that

in all members of the subfamily Cynanchoideae previously investigated the anthers are bilocular, the case of *Secamone* becomes most interesting.

Demeter (1922) is the only recent morphologist to deal in detail with evolutionary trends in the closely related families Apocynaceae and Asclepiadaceae. One of the points he raised was the problem of the derivation of the bilocular anther of the subfamily Cynanchoideae from the basic 4-locular type shared by other Apocynales. Demeter, unfortunately, was unable to obtain either fresh or preserved material of the critically important genus *Secamone* to complete his studies; consequently, no developmental studies of the floral parts was possible. This led him to purely tentative conclusions. He advanced two explanations for the paired pollinia of *Secamone* anthers and wrote

> "Es ist fraglich, ob dies ein Zeichen fur Primitivität ist, insofern, als es hier noch zu keiner Reduktion gekomen ist, oder ob sich hier die pollinien, frühe rauch einfach, nun sekundär wieder, etwa durch eine, falsche Scheidewand."
> (It is questionable whether this is an indication of primitiveness, insofar as here it has still arrived at no reduction, or whether the pollinia, still simple in early development have perhaps become doubled secondarily by a false secondary wall.)

Demeter apparently favored the second hypothesis. He mentioned the case of *Thevetia nereiifolia*, an apocynaceous plant. Here, he observed, the whole contents of the pollen sac do not develop into pollen but, in the formation of pollen mother cells, patches of tissue remain sterile and grow in bridge-like manner from one wall to the other of the pollen sac, just as in certain Onagraceae. Demeter continued with his conjecture and maintained that, perhaps in the same manner, the pollinia of *Secamone* could have become doubled by a false partition (as in certain ovaries), the polliniferous plates assuming a complanate position.

Such a purely hypothetical conclusion cannot be accepted unless it is supported by anatomical evidence. With this in mind an attempt was made to secure buds and flowers of species of the genus *Secamone*. Alcoholic preserves of flowers and floral buds were sent from the Royal Botanic Gardens, Kew, by the Director, Sir George Taylor, to whom I am particularly grateful. My thanks are also due Dr. H. Wild, of the Southern Rhodesia Government Herbarium, for preserved buds and flowers of *S. frutescens*, and Dr. R. A. Dyer, Director of the Botanical Survey of the Union of South Africa, for preserved material of *S. alpinii*.

Special attention was paid to the ontogeny of the anther, pollinia and the stigma head. The study then was extended to cover vascular anatomy and general morphology of the flower. The results obtained revealed interesting evolutionary information which was then applied to certain other groups in the Apocynaceae and Asclepiadaceae as well. From the comparative morphology and ontogeny of these groups certain new approaches to the problems of anther locule suppression, translator specialization, pollen formation and coronal evolution were possible.

Materials and Methods

Serial transverse and longitudinal sections of flowers and floral buds of the species studied were prepared from material preserved in formalin-aceto-alcohol. The preserved material was embedded in paraffin either by the standard alcohol-

xylene method or through the tertiary butyl-ethyl alcohol procedure. Microtome sections were 6-10 μ; aqueous crystal violet and erythrosin in clove oil produced satisfactory staining, rendering vascular tissue quite distinct. Fast green in clove oil and safranin (Johansen's methyl cellosolve formula) gave satisfactory results with the pollinium sacs and the translators. Harris' haematoxylin was also employed.

The species which were studied are listed below together with their sources and collectors, with their numbers whenever available.

Species	Source	Collector & Numer
Secamone alpinii Schult.	Botanical Survey of the Union of South Africa	
S. frutescens Decne.	The Southern Rhodesia Government Herbarium.	
S. afzelii (R. & S.) K. Schum.	Royal Botanic Gardens, Kew.	*Onochie, F. H. I. 33276*
S. myrtifolia Benth.	Royal Botanic Gardens, Kew.	*Milne-Redhead 5116*
S. platystigma K. Schum.	Royal Botanic Gardens, Kew.	*Dawkins 610*
S. punctifolia Decne.	Royal Botanic Gardens, Kew.	*Drummond & Hensley 3617*
S. stenophylla K. Schum.	Royal Botanic Gardens, Kew.	*Drummond & Hensley 2769*
S. stenophylla K. Schum.	Royal Botanic Gardens, Kew.	*Faulkner 1718*
S. stuhlmannii K. Schum.	Royal Botanic Gardens, Kew.	*Milne-Redhead & Taylor 7597*
S. zambesiaca Schult.	Royal Botanic Gardens, Kew.	*Wild, S. R. G. H. 22621*
S. sp.	Royal Botanic Gardens, Kew.	*Drummond & Hensley 2794*
Periploca graeca L.	Cornell University	*H. E. Moore, Jr.*
Hemidesmus indicus R. Br.	Poona, India	*U. R. Desphande 60963*
Gonolobus barbatus H. B. & K.	Nayarit, Mexico	*Dressler & Wirth 2719*
Matelea quirosii (Standl.) Woods.	Michoacán, Mexico	*Dressler & Wirth 2747*
M. carolinensis (Jacq.) Woods.	Gray Summit, Missouri	*Safwat*
Cynanchum laeve (Michx) Pers.	Washington University, St. Louis, Missouri	*Safwat*
C. laxum Bartl.	Missouri Botanical Garden, St. Louis, Missouri	*Safwat*
Sarcostemma clausum (Jacq.) Roem. & Schult.	San Luis Potosí, Mexico	*Hewitson & Hunter 85*
Asclepias curassavica L.	Missouri Botanical Garden, St. Louis, Missouri	*Safwat*
Apocynum cannabinum L.	Gray Summit, Missouri	*Safwat*
Vinca rosea L.	Florida	*Woodson*

Floral Morphology and Anatomy of Secamone

The calyx lobes are small, almost free and imbricate. Within them at the base a number of small glands are found. The corolla is gamopetalous, 5-parted, rotate or campanulate and contorted in aestivation. Frequently below the sinus

of the lobes one finds protuberances from the corolla tube, giving the appearance in serial sections of a corolline corona, as is well seen in *S. stenophylla* and certain other species.

The stamens are epipetalous with very short filaments which are free from one another or united for a very short distance. The anthers have very short lateral wings and are usually terminated by a small hyaline appendage which becomes inflexed upon the stigma head; the dehiscence is longitudinal. The staminal corona segments, rather simple filaments, are free from one another and attached to the staminal column or higher up the stamens, frequently bent inward and sickle-like, or are represented by a small hump on the dorsal side of the stamens.

Although the anthers of practically all species of *Secamone* have a thin hyaline apical appendage, that of *S. frutescens* differs in that the cells are glandular; it is not difficult to observe the secretion since it fixes in FAA and stains with safranin.

The two carpels usually are more or less subinferior and united only at their stylar regions, where, together, they form the stigma head. The stigma head consists of a lower trapezoid structure of various configuration; above this it is sharply constricted and may be cylindrical-fusiform, as in *S. zambesiaca* (plate 2, fig. 1), *S. afzelii* and *S. myrtifolia,* or abruptly enlarged and broadly 2-lobed, as in *S. frutescens, S. platystigma, S. punctifolia,* and *S. stenophylla.* Within the ovaries the ovules are anatropous and borne on submarginal placentas.

In all the species studied the relative position of the stamens to the stigma head is the same, the anthers being slightly above the trapezoid body and forming jointly the well-known gynostegium of the milkweeds.

Vascular Anatomy—Two different patterns of vasculature were observed in the flowers of *Secamone* with many intermediate types in between. These two extremes are represented by *S. frutescens* and *S. stenophylla.* In the former the vascular supply to the calyx lobes is the 3-trace 3-lacunar type while in the latter it approaches the 1-trace 1-lacunar condition. The anatomy of these species will be discussed separately since they show other significant differences in their floral organization.

Secamone frutescens—The pedicel of a flower of *S. frutescens* is terete and has an amphiphloic siphonostele corresponding to that of a young stem of the plant, the xylem being embedded in a cylinder of protophloem parenchyma. The vascular cylinder superficially appears dissected and not continuous due to the fact that certain provascular cells have not been differentiated into xylem elements. Outside the vascular cylinder there are patches of laticiferous tissue.

The pedicellar wood consists chiefly of protoxylem with relatively scant development of metaxylem, no vessels being observed and the secondary walls of the tracheids being either spirial or annular.

The pedicellar stele expands and abruptly becomes increasingly lobed with five distinct and five alternate and less distinct salients becoming increasingly prominent. At this level the pedicel further expands together with the stele, and the traces begin to diverge; thus transition of the pedicel into the receptacle becomes clear.

Five traces will form the midribs of the calyx lobes (text-fig. 1) and almost immediately above them five other traces leave the stele and traverse the receptacle for a short distance. Then each gives rise to two lateral traces, one of which will form the lateral bundle of one of the calyx lobes while the second will form the lateral bundle of the adjacent lobe. Thus, the calyx laterals are adnate to the corolla midribs, as also has been reported for certain Apocynaceae by Woodson and Moore (1938). Upon the departure of the calycine traces, phloem strands can be seen leaving the inner faces of the stelar phloem and invading the pith where they branch and anastomose as was also reported by Scott and Brebner (1891) in the stems and roots of certain Gentianaceae, Apocynaceae, Solanaceae and Plumbaginaceae. Woodson and Moore have observed the same in the pedicel and receptacle of certain genera of Apocynaceae.

After the departure of the calycine traces there appear 10 bundles, five large, which are destined to supply the stamens and five alternate and small, which will furnish the five corolline traces (text-fig. 1). At this level also a residual stele can be seen, in the center of the receptacle, which will supply the walls of the carpels and the ventral traces of the ovules. This is substantiated by the fact that the constitution of the residual stele is soon followed by the appearance of the two ovarian cavities. Soon the anatropous ovules make their appearance in the section.

It is interesting to note that the placentas, although described in the Asclepiadaceae as well as in Apocynaceae as marginal, are in reality submarginal. The ovules are not borne on the whole surface of the placentas but rather on the inner side only (plate 2, fig. 2). Thus, there can be seen in serial sections that two small margins of each placenta are devoid of ovules. It is worth mentioning here that the sterile margins of the placentas are directed upwards instead of in the usual downward direction seen in Asclepiadaceae and Apocynaceae. This is also found in *Mandevilla,* an apocynaceous plant (see Woodson and Moore, plate 5). Baum (1949) by means of growth studies on younger stages of *Cynanchum vincetoxicum, Asclepias syriaca,* and *Erythraea centaurium,* showed that placentas of these plants are not inwardly folded carpel margins but arise from the submarginal upper face of the carpel; hence the placentas should be called submarginal.

While the two stamen bundles are giving rise to the two carpel dorsals, the calyx lobes begin to separate from the receptacle. This separation is continued while the two carpel walls are still united with the surrounding tissue. It is clear that the carpels are more or less subinferior, a character not found in other Asclepiadaceae but usual in Apocynaceae (Woodson, 1935). Soon the two apocarpous carpels start separating from the corolla-staminal tissue; at the same time the calyx lobes are completely freed from the corolline ring.

On the inner surfaces of the calyx lobes a number of small glands called "squamellae" are found. In this species, as in several others in the genus *Secamone,* the calycine squamellae are usually on three of the five calyx lobes; the outer are devoid of them. Each gland consists of a central core surrounded by a palisade layer of glandular epidermal cells. No vascular tissue was observed in these small

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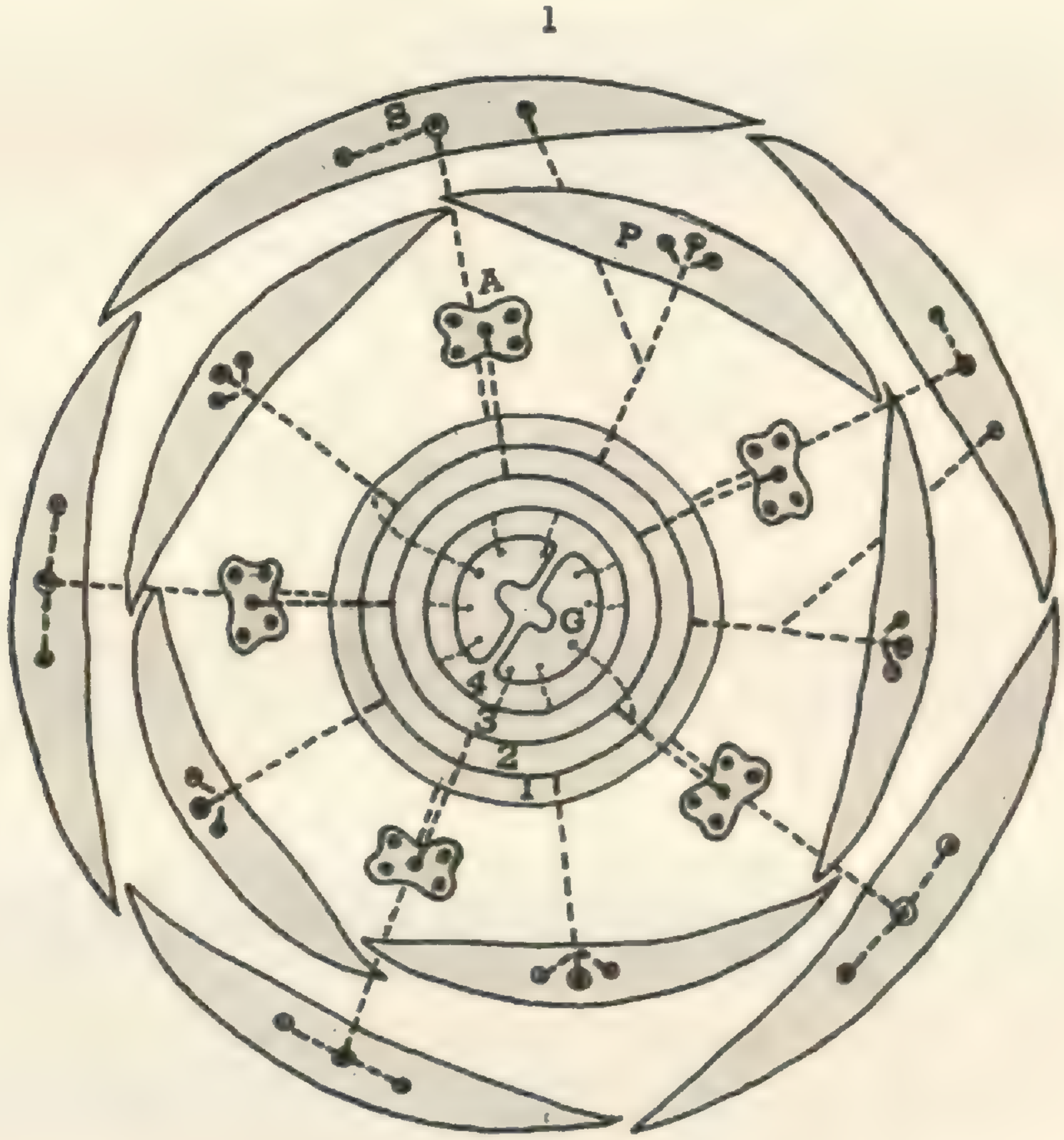

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Text-fig. 1. Diagram of the floral vasculature of *Secamone frutescens.*
Text-fig. 2. Diagram of the floral vasculature of *Secamone stenophylla.* S: calyx lobes, P: corolla lobes, A: stamens, G: carpels, 1-4 consecutive residual steles.

bodies. Similar glands have been reported in Apocynaceae (Woodson and Moore 1938), and Asclepiadaceae (Woodson 1933, 1941, 1954; Holm 1950 and others).

Squamellae have been interpreted as modified stipules in Apocynaceae by Woodson (1930, 1938), a hypothesis which may also be applied to the obviously homologous glands of *Secamone.*

When separation of the carpels from the staminal-corolline tissue is completed, the five corolline bundles give rise to their lateral traces. Soon the styles of the two carpels unite to produce the stigma head, and the stamens become freed from the corolla. It can be seen in serial sections that the stamens are close to the stigma head with no adnation apparent.

The wings of the adjacent anthers, jointly with the stigma head, form the stigmatic alar chambers. Five interrupted patches of the epidermal cells of the stigma head in all species sectioned, save *S. frutescens,* become protuberant and project into the five alar chambers. In the latter species the entire epidermal layer of the stigma head becomes papillate. And, as one approaches the regions of the stigma head which bear the translators, not only the cells of the stigma head become protuberant but also the adjacent cells of the stamens; this is a well-known character in many Apocynaceae. Frye and Blodgett (1905) described the relationship between the anthers and the stigma head of *Apocynum* thus

> "Immediately beneath the anther locules is a beard of epidermal hairs extending transversely across the faces of the anthers, forming a ring around the stigmatic head (figs. 1, 2, b). These hairs meet similar ones from a ring around the head, thus preventing pollen from falling into the base of the flower."

This situation is another primitive feature retained in *Secamone* although in a reduced, nonfunctional state.

At a slightly higher level the stamens become appressed about the stigma head but not adnate—thus, the gynostegium. Soon the region of the translators appears in the sections followed by the appearance of 20 pollinium sacs, two in each anther lobe.

Secamone stenophylla—The pedicel of a flower of *S. stenophylla* is an amphiphloic siphonostele like that of *S. frutescens.* The stele expands below the receptacle and becomes 5-lobed, contrasting with the 10-lobed stele of *S. frutescens.* From the five angles of the stele five traces leave and supply the calyx lobes (text-fig. 2). The origin of the lateral traces of the calyx lobes, however, differs from that of *S. frutescens;* a lateral trace of one of the outer calyx lobes arises from a corolline bundle while the other lateral trace of the same lobe is derived from its own midrib. Similarly, one of the inner calyx lobes receives one of its lateral traces from a corolline bundle and the other from its midrib. The remaining three lobes receive their lateral traces from their own midribs. When the calycine traces leave the stele, there remain 10 bundles, five large, and five alternating and smaller; these are the staminal and corolline bundles respectively.

The ovarian cavities make their appearance rather high in serial sections and their walls are supplied by many slightly lignified bundles. The origin of the

dorsal bundles of the two carpels is different. One of the carpels receives its dorsal trace from a staminal bundle, while the other receives its dorsal trace from a corolline bundle. The apocarpous carpels are united with the staminal filaments slightly above the receptacle.

As the carpels free themselves from the staminal filaments, the corolline bundles give rise to their lateral traces, and the epipetalous stamens become separated from the corolla tube; at this level the carpels become close to one another and finally fuse to form the stigma head. The stamens soon become appressed to the stigma head, unlike those of *S. frutescens,* but still there is no adnation. The areas of the stigma head between the adjacent anther wings show marked protuberances, and these project into the alar chambers. At this level, also, the five corona lobes become separated from the stamens. The corolla tube is provided with about 15 more or less conspicuous vertical ridges which are considered as a corolline corona by some authors.

Calycine Vasculature of Other Species—Several intermediate types of vasculature occur between the two extremes just mentioned. For example, in *S. myrtifolia* one of the outermost calyx lobe traces gives rise to a lateral trace of the adjacent lobe; in *S. zambesiaca* one of the lateral traces of the calyx lobes arises independently from the stele while the dorsal bundles of these lobes give rise to the other lateral trace of each lobe; an innermost lobe, however, recieves a single trace which in turn forms its own laterals. In the few examples of calycine vasculature mentioned, one can follow a gradual trend from the strictly 3-trace 3-lacunar type to a condition which approaches the 1-trace 1-lacunar condition. Woodson and Moore have classified an assemblage of genera and species of Apocynaceae with a combination of different types of calyx vasculature under their type IV; they would consider the type represented by *S. frutescens* as more primitive than the types which approach the 1-trace 1-lacunar condition predominant amongst the majority of Gamopetalae.

Ontogeny of the Pollinium Sacs—In a cross section of a very young anther of *S. frutescens* no differentiation of the sporogenous tissue is apparent (text-fig. 3). In a later stage, however, four plates of hypodermal cells become apparent at the four angles of the anther, each 3-4 cells long (text-fig. 4). These are the archesporial cells; and, hence, a 4-locular condition is evident from the beginning. These hypodermal cells undergo a tangential division to produce a primary parietal layer outward and a primary sporogenous tissue inward (text-fig. 5). The cells of the outer layer divide both tangentially and anticlinally to produce from 3-4 layers, the innermost of which is the uninucleate tapetum (text-fig. 6 and plate 3, fig. 1). A few cells on the inner side of the primary sporogenous tissue undergo division to produce the inner tapetum, which is frequently 1-2 layers thick. Thus the tapetum has two different origins and evidently serves, through differing secretions, both for nutrition of the developing pollen cells and as a binding substance for the resulting tetrads to group them into the pollinium sacs.

The primary sporogenous cells act directly as pollen mother cells without giving rise to daughter cells. There are from 3-4 pollen mother cells within each

anther loculus and these are radially elongated (plate 3, fig. 2). However, unlike other members of the Cynanchoideae, the two ends of the pollen mother cells are not always the same in width and the shapes of the cells are complementary one to another. The two outer cells are more or less similar in width at both their upper and lower ends, while the middle cell has one end narrow and the other, wide.

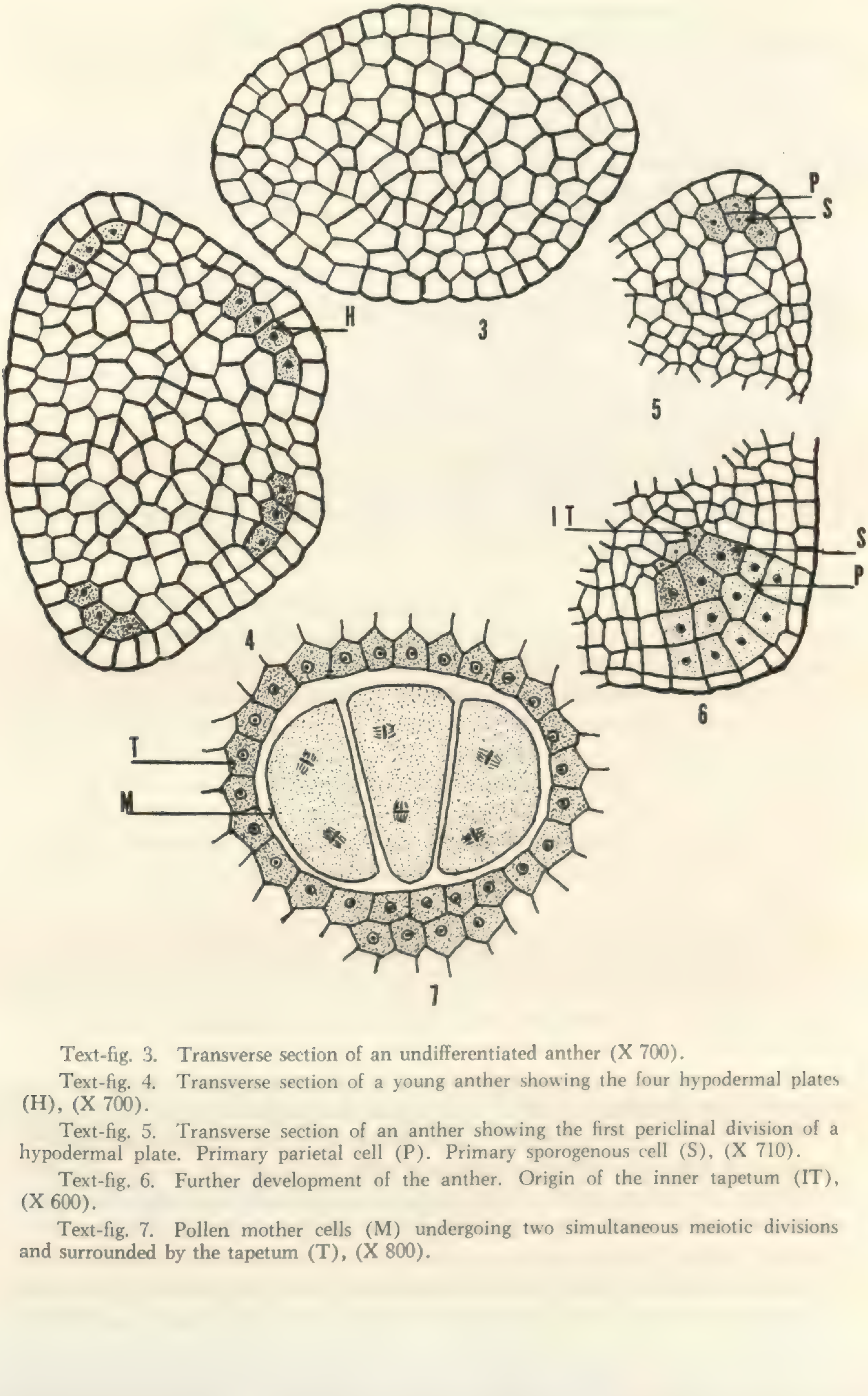
The nuclei of the pollen mother cells undergo two simultaneous meiotic divisions as seen in text-fig. 7; cell wall formation between the four daughter nuclei is slightly delayed. The ultimate configuration of the resulting tetrads depends upon the direction of the second meiotic spindle. Accordingly, the two lateral pollen cells form a rhomboidal tetrad while the middle result in a T-shaped tetrad (plate 3, figs. 3-4).

The tapetum persists for some time after the formation of the tetrads, which are not separated from one another but continue to lie in a solid mass. The thin walls of the pollen mother cells stain with fast green in the early stages of their maturation; but, as the tapetum becomes disorganized, the outer walls of the pollen mass, as well as the walls within, become thickened and show strong affinity for safranin. At maturity, each tetrad of pollen is enclosed within its compartment of thickened walls. Besides these common walls, each individual pollen grain has its own thin intine. When the pollinium sacs are mature, the anthers dehisce longitudinally by means of hypodermal mechanical cells as in the Apocynaceae and the subfamily Periplocoideae of Asclepiadaceae, in contrast to the apical pores of the majority of Cynanchoideae of the latter family.

The pollinium sacs of most of the species are more or less globular, each translator carrying four sacs belonging to two adjacent anther halves; but in *S. alpinii* and *S. myrtifolia* they are elongated. In serial transverse sections of the anthers with globular pollinia the four anther locules appear all at the same level; where pollinia are elongated, the locules appear in serial transverse sections at two different levels. The inner locules (the ones closest to the stigma head) are vertical and the pollinium sacs are erect within them, but the outer locules and their included pollinium sacs are obliquely horizontal. Upon attachment to the translator, however, both inner and outer pollinium sacs become horizontal due to inflexion of the anthers.

Ontogeny of the Translators—The development of the translators was followed in *S. frutescens* and *S. alpinii*. In a young bud of the latter (slightly less than 1 mm. in diameter), the stigma head shows a roughly circular contour surrounded by closely packed glandular epidermal cells slightly below the level of the anther locules. The anthers are closely appressed to the stigma head, but their is no adnation. At such a level, the stigma head is provided with five vertical protuberances between the adjacent anther wings. As the two lobes of the stamens become clear in serial sections, the stamens become appressed to the stigma head at only 10 points of the anther lobes. The five grooves of the stigma head between the adjacent anthers, so customary in mature flowers, are not differentiated until the time at which the pollen is fully mature.

At the time of pollen development the five grooves of the stigma head are lined with closely-packed glandular cells (plate 5, fig. 2). These cells stain darker



Text-fig. 3. Transverse section of an undifferentiated anther (X 700).

Text-fig. 4. Transverse section of a young anther showing the four hypodermal plates (H), (X 700).

Text-fig. 5. Transverse section of an anther showing the first periclinal division of a hypodermal plate. Primary parietal cell (P). Primary sporogenous cell (S), (X 710).

Text-fig. 6. Further development of the anther. Origin of the inner tapetum (IT), (X 600).

Text-fig. 7. Pollen mother cells (M) undergoing two simultaneous meiotic divisions and surrounded by the tapetum (T), (X 800).

than the rest of the epidermal cells in *S. alpinii;* in *S. frutescens,* the contrast is not so pronounced. The lateral margins of the five stigmatic grooves show a yellowish lipoid secretion in two bands (plate 4, fig. 1); these bars, stained lightly with safranin, did not take a crystal violet-erythrosin combination.

As the buds develop further, the secretion of the same substance is continued by the deeper cells of the grooves, apparently secreting the same lipoid compound. Thus, in a later stage, there can be seen in sections five small horseshoe-shaped, noncellular bodies near the stigma head (plate 4, fig. 2). While the buds approach maturity the secretion of the stigma head continues, but the secretion is not as firm as previously. As the stigma head continues to secrete the translators, the products thus formed are pushed outward and slightly upward; at this time also, the areas opposite the anthers secrete similar material. The substance thus secreted by the stigma head is accumulated between the anther lobes as five small bodies similar in their staining reaction with safranin to those secreted by the five grooves (plate 4, fig. 4).

It is curious to note that the translators are very close to the anther wings at maturity, and the tips of the latter actually can be seen—in serial sections—to be attached to the dorsal slits of the translators. This might be a means by which the anthers give some support to the translators to keep them in proper position for the insect visitors.

When mature flowers were sectioned, the entire surface of the stigma head at the level of the five grooves showed a foamy secretion staining with fast green in contrast to the firmer safranin-staining bodies first produced; above this level, however, the horseshoe-shaped bodies appeared in sections which previously had been pushed upward and outward (plate 4, fig. 3). At the time of complete maturity the pollinium sacs are attached to the portions of the translators nearest them at the dehiscence of the anthers. This attachment is either vertical, as is the case in most of the species sectioned, or horizontal as in *S. alpinii* and *S. myrtifolia* (plate 2, fig. 4). In the latter, the four horizontally-elongated pollinium sacs can be seen occupying two different levels and appear in serial sections one at a time in either anther lobe.

Pollinium and Translator Development in Other Asclepiads

An evaluation of the floral mechanism of *Secamone* and an appreciation of the floral evolution of the Asclepiadaceae must be based upon comparative studies of both more primitive and more advanced genera. For this purpose I have selected *Periploca graeca,* of the Periplocoideae, and *Asclepias curassavica* and *Cynanchum laeve,* of Cynanchoideae.

Periploca graeca—The ontogeny of the anthers of *P. graeca* is essentially as it is in *Secamone,* except that the four archesporial plates are each from 10-12 cells long and that in the formation of the inner tapetum many cell divisions take place. The entire tissue embraced by the concavity of the sporangia acts as inner tapetum (plate 6, fig. 4). This conclusion is supported by the fact that the nuclei of these cells are paired, as are those of the 1-layered outer tapetum; and, at a later stage of development, the cell walls of this tissue become extremely delicate and difficult

to distinguish. Similar observations have been made by Rao and Rao (1954) on *Cryptostegia grandiflora* of the same subfamily. In *Vinca rosea*, an apocynaceous plant, Boke (1949) observed that

> "Within the sporogenous cells, deeper cell layers contribute to the tapetum and in this region it is frequently more than one layer in thickness,"
>
> which I have corroborated (plate 6, fig. 3).

The primary sporogenous cells may undergo periclinal division to form elongate daughter cells which serve as pollen mother cells; or, more often, they themselves act directly as pollen mother cells. In either event they undergo two simultaneous meiotic divisions, as in *Secamone*, various Apocynaceae, and other members of the subfamily Periplocoideae of Asclepiadaceae. The resulting pollen tetrads are tetrahedral and isobilateral together with some intermediate types depending on the direction of the second meiotic spindle. Similar observations have been made by Rao and Rao (1954) on *Cryptostegia grandiflora*, and by Nirulla and Richharia (1945) on *Hemidesmus indicus* of Periplocoideae and by Sax and Husted (1936) on *Periploca sepium*. In the latter two species, however, the authors have reported also the presence of linear and T-shaped tetrads in one and the same anther locule.

The ontogeny of the translators of *P. graeca* was extensively and correctly studied by Demeter (1922). I have nothing to add to his basic findings, although a few additional details which lend significance to a later discussion should be added here.

The translators of the Periplocoideae are rather unique in both structure and development. A translator almost always consists of an open cartilagenous shovel- or cornucopia-like structure which is lined with a foamy secretion and, at maturity, receives pollen tetrads from adjacent anther halves. Below this is a stalk which ends in a basal adhesive disc (plate 5, fig. 4). Both the stalk and the disc aid the process of pollination through the insect visitors. Delpino (1867) has described this process and found that, when an insect visits a flower of *Periploca*, the adhesive disc may become attached to its tongue or other parts of its body by the sticky surface. As the insect removes a translator the stalk becomes bent; and, when another flower is visited by the same insect, the shovel and its pollen may become inserted between any two adjacent anthers upon the receptive surface of the stigma head.

Ontogenetic studies of the translators reveal that the secretion of the translators is restricted to five vertical grooves of the stigma head (plate 5, fig. 3). The side walls of each groove commence secretion at only four isolated marginal points—two at the upper end of a groove, and two at the lower. Later, two patches of deeper glandular cells at both ends within the grooves begin to secrete similar material; thus bring together the previously secreted pairs of plates. An essential difference between the order of secretion of upper and lower parts of a translator is that in the former the first-secreted substance of the stigma head is a foamy-alveolar type and stains with fast green. This substance is important because it lines the shovel of the translators and thus aids in keeping the pollen tetrads adhering to its surface. This frothy substance is then followed by another secretion from the

same glandular cells of the stigma head, except that this new secretion is a more or less solid substance which stains with safranin. From the two substances, and in the order of secretion just mentioned, the shovel is produced. The lower portions of the five grooves of the stigma head also are lined with glandular cells; but the order of secretions is reversed—first hard, then foamy. The first solid compound is pushed outward and slightly upward by a more alveolar substance secreted by the same cells. The lower portion of the translators consists of the stalk and an adhesive disc. At maturity, the shovel and the stalk are joined and the process of translator formation is completed.

Asclepias curassavica—Woodson (1954) studied the ontogeny of the pollinium sacs of four species of Asclepias. He pointed out for the first time that the tapetum on the dorsal side of each locule is massive while that on the ventral side is uniseriate or at most biseriate, and that there are two distinct functions reflected in this differentiation. Woodson's observations agree with the organization mentioned above for *Periploca graeca* and *Cryptostegia grandiflora*. I have observed the same in species of *Cynanchum* and *Matelea* as well as in *Asclepias curassavica*.

The ontogeny of the anthers of *A. curassavica* is essentially as that in *Secamone* except that only two archesporial plates are developed, which anticipates the presence of but two locules (plate 6, fig. 1).

The tapetum of the dorsal half of each anther locule, which is derived from the plate of cells dorsal to the primary sporogenous tissue, becomes massive and multiseriate (plate 6, fig. 2). As the tapetal cells develop further, they become vacuolate and contain certain lipoid bodies which stain very prominently with safranin. This was first observed by Woodson (1954) in *Asclepias*. I have observed the same in species of *Cynanchum* and *Matelea* as well as in *Asclepias*. At maturity, both the ventral and the dorsal tapetum become disorganized but the latter persists for some time after the disappearance of the former—as in *Periploca*. The cells become 1- to 3-nucleate at maturity and the cell walls become increasingly delicate. The tapetum of the milkweeds as well as of the apocynads is the secretory type and in *Asclepias*, as in *Secamone*, it is highly evolved, certainly performing a dual function; thus it seems that the ventral tapetum serves as a nutritive source for the development of the pollen, whereas the dorsal contributes to the formation of the pollinium sac membrane and in binding the pollen tetrads together.

The primary sporogenous cells act directly as pollen mother cells without giving rise to daughter cells. These cells undergo striking radial elongation. Each mother cell undergoes two meiotic divisions which are successive. Thus, after the first division, a cell wall is formed between the resulting diads (plate 6, fig. 2); the other division takes place to produce the tetrads. The tetrads in *Asclepias*, as well as in other genera of the subfamily Cynanchoideae except *Secamone*, are linear in their composition, the two meiotic spindles being parallel to the long axis of the pollen mother cells. Further details of development of the pollinium sacs are found in Woodson's work (1954) as well as in that of others.

Cynanchum laeve—The ontogeny of the translators of *C. laeve* is quite similar to those of *Asclepias cornuti* (=*A. syriaca*) studied by Corry (1883) and of *A. curassavica* by Woodson (1954).

In very young buds of *C. laeve* the stigma head consists, in cross section, of a roughly circular structure with no trace of the system of grooves so characteristic of this organ in mature buds; at this time it does not seem to be different from that of Apocynaceae and other Asclepiadaceae. Soon, however, five primary vertical grooves become differentiated and from either side of each there develops secondarily a less-pronounced, obliquely descending furrow (text-fig. 15). The primary grooves as well as the secondary furrows are lined with many narrow, compactly-arranged cells which stain prominently with safranin.

The first indication of the translator apparatus is initiated as two lines of lipoid substance secreted by the margins of the five grooves. This is continued until finally the inner cells of the grooves join in the secretion as well. This structure, which is the corpusculum or "gland," is 2-parted in early stages of development and, consequently, has a dorsal slit at maturity. The dorsal slit aids in the withdrawal of the pollinium by becoming the organ of attachment to the body of insect visitors. At maturity the corpusculum becomes dark brown and is very hard, with vertical striations corresponding to the cells of the grooves which have secreted them. The cells of the lateral secondary furrows secrete a less rigid substance to produce the translator arms. (text-fig. 14).

Discussion

Except for the small tribe Secamoneae, the anthers of all members of the subfamily Cynanchoideae of Asclepiadaceae have but two locules. In this tribe, however, as well as in the subfamily Periplocoideae and in all Apocynaceae, the anthers are 4-locular. The question arises whether there is any evidence of suppression or fusion of microsporangia in early stages of development of the anthers of Cynanchoideae.

Several morphologists have investigated this problem—Frye (1901), Gager (1902), Richharia (1934) and others—but almost all agree that there is no evidence provided by ontogenetic studies of several genera. Engler (1876) came to the empiric conclusion that only the anterior locules are developed and believed that the posterior locules become diverted to the formation of the hyaline appendage of the anthers. Demeter (1922) came to the conclusion that the outer locules have been transformed into the lateral anther wings of the Cynanchoideae which he calls "Leitschienen." Both assumptions seem wholly gratuitous in the complete absence of evidence of such transition.

Demeter (1922) attacked the problem of suppression of anther locules through the study of the closely-related family Apocynaceae, finding that, in the Plumerioideae, the four locules are filled with pollen whereas, in the more advanced subfamily Echitoideae, the posterior locules are partially empty while the anterior are more fully developed. From such observations he concluded that, perhaps in the same way, the bilocular anthers of the Cynanchoideae may have been derived.

My own studies tend to confirm the view that the 2-locular anthers of Cynanchoideae have been derived from a primitive 4-locular condition, but from other considerations. First, the two hypodermal archesporial plates appear in exactly the same position as do the ventral pair of locules in the Periplocoideae, *Secamone,* and Apocynaceae. It seems that suppression of the two locules of the anthers of Cynanchoideae is due simply to the failure of the corresponding hypodermal plates to differentiate in the early ontogeny of the anthers. It is not necessarily true—as Engler and Demeter assumed—that a lost plant organ must be transformed to perform another function. Second, the staminal bundle of all bilocular anthers of Cynanchoideae occupies a position very close to the dorsal epidermis of each anther and dorsal to the locules, while the same bundle occupies a position nearly between the dorsal and the ventral anther locules in the 4-locular anthers. The most interesting evidence to support the assumption of a suppression of the dorsal locules is derived from the origin of the complementary layers of tapetum in the anthers of both Asclepiadaceae and Apocynaceae.

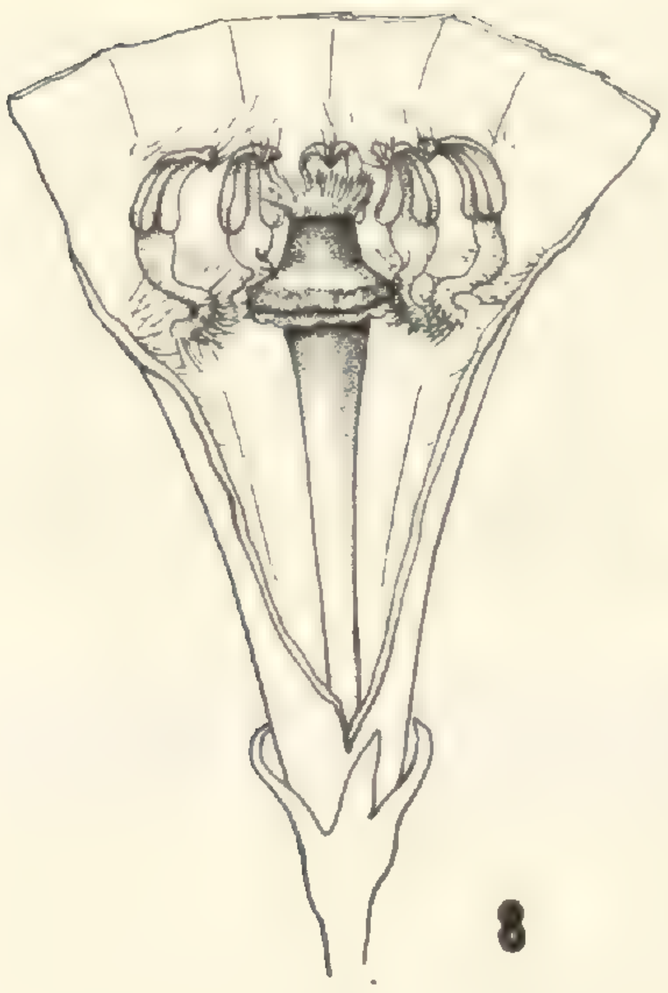
The dual origin of tapetum in many families of flowering plants is a well-established fact which is best expressed by Macré and Thomas (1930), who wrote

> "Les tapis externe tire son origine, comme les cellules mères primordiales du cloisonnement de l'assise staminale sousépidermique . . . . Les cellules qui constituent ce que nous appelons le tapis interne, elles, tirent leur origine de cellules banales du connectif. Malgré cette diversité d'origine, elles évolueront exactement de la même manière que les cellules du tapis extèrne; souvent même (Solanum Dulcamara L., par exemple), ces caractères speciaux appaissent d'abord dan les cellules du tapis interne."

Frequently the inner tapetum of the Asclepiadaceae and Apocynaceae is more than one layer thick. In certain genera as *Asclepias, Periploca,* and *Cryptostegia,* the inner tapetum of the anther locules is very massive. In *Asclepias,* the inner tapetum of the two locules is oriented toward the vascular trace (i.e., dorsally), creating the impression that they represent the ventral locules of primitive 4-locular anthers, with the two dorsal locules having disappeared without a trace. This conclusion is based on a comparative study of *Periploca* where there are four anther locules with the tapetum in all cases oriented toward the vascular bundle.

An interesting aspect of the ontogeny of the anthers of *Secamone* is the development of the pollinium sacs. A pollinium, in a general sense, consists of a body of tetrads which are transferred en masse in pollination. This structure so characteristic of the Cynanchoideae is not restricted to this group, however.

In the Apocynaceae the pollen at maturity is usually granular but remains in tetrads in certain genera of both Plumierioideae and Echitoideae (e.g., *Condylocarpon* and *Apocynum,* respectively). In Periplocoideae of Asclepiadaceae, the pollen grains are in tetrads but not enclosed within sacs, while in Cynanchoideae they are enclosed within definite chambered sacs. In Orchidaceae close parallelism may be found. Swamy (1949) has reported in some genera of Orchidaceae, as *Cypripedium* and *Vanilla,* that the pollen grains separate from one another and become free. In *Pogonia* the four cells of a tetrad adhere to form a "compound grain." In the tribe Orchideae (Ophrydeae) and Neottiae this tendency is carried



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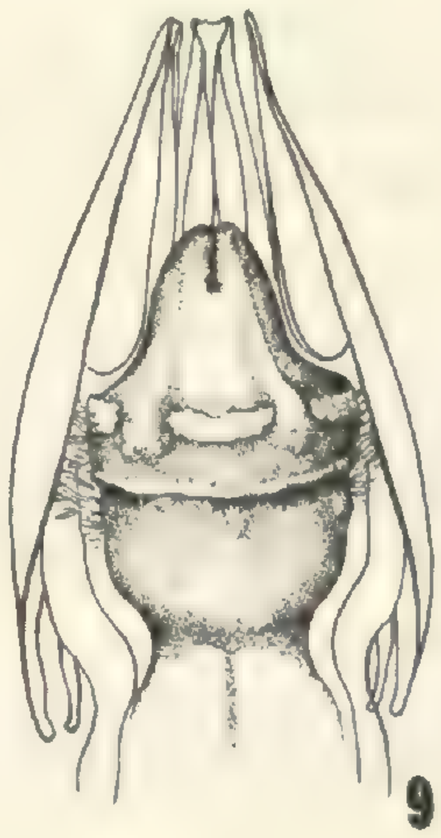

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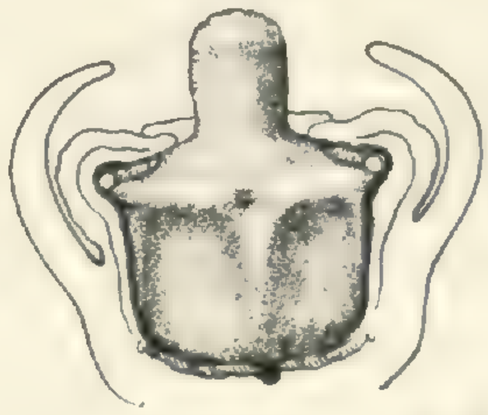

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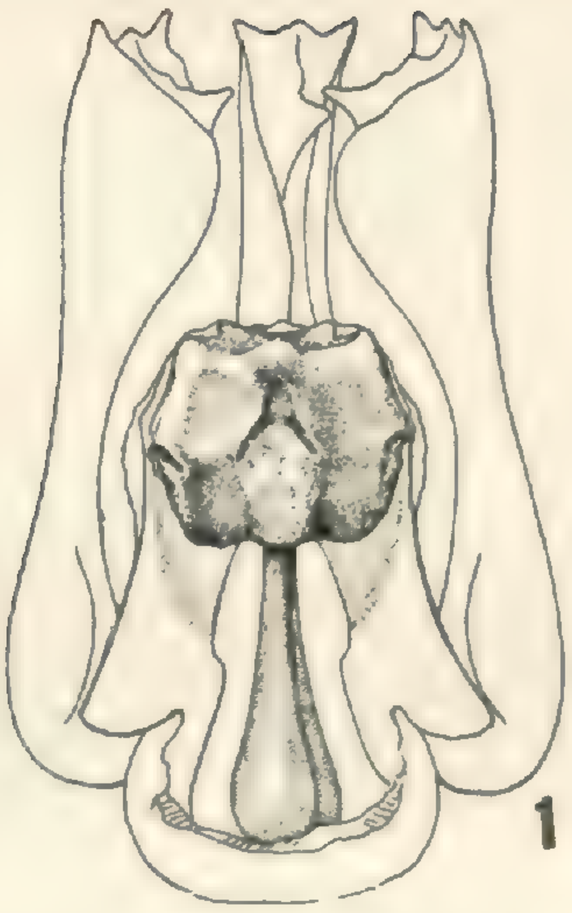

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Text-fig. 8. Flower of *Vinca minor* longitudinally opened to show the relationship of the anthers and the stigma head (X 4).

Text-fig. 9. Flower of *Apocynum cannabinum* with two stamens removed to show the plates secreted by the stigma head (X 10).

Text-fig. 10. Flower of *Periploca graeca* with two stamens and one pollinium removed; two pollinia are in position within the grooves (X 5).

Text-fig. 11. Pollinium of *Secamone alpinii* (X 140).

Text-fig. 12. Flower of *S. alpinii* with two stamens removed, as in fig. 10 (X 14).

Text-fig. 13. Pollinium of *P. graeca* showing the shovel, stalk and adhesive disc (X 30).

Text-fig. 14. Pollinium of *Asclepias subulata* (X 16).

Text-fig. 15. Flower of *A. subulata* with two stamens removed to show the primary and two secondary furrows above the receptive surface of the stigma head (X 4).

Text-fig. 16. Two adjacent anthers of *A. subulata* to show their relationship to a pollinium (X 10).

farther, and the compound grains are themselves held together into mealy pollinia (which in the Orchideae are divided into small units called massulae). In *Coelogyne* and *Pholidota,* the microspore mother cells and their derivatives remain together and continue their development as a single unit; in more advanced genera, such as *Oncidium* or *Vanda,* the pollinia develop as coherent units and become quite hard in texture.

Pollinium formation is reported to occur in other families of the flowering plants, as in the subfamily Mimosoideae of the Leguminoseae, in Chlaenaceae, and in several genera of Ericaceae and Juncaceae.

In the majority of the Apocynaceae the simultaneous pollen mother cell division is predominant. Frye and Blodgett (1905) observed this in *Apocynum,* Täckholm and Söderberg (1918) in *Vinca,* Rau (1940) in *Cerbera* and *Vallaris* and in many species investigated by Schürhoff and Müller (1937). Meyer (1938) reported the occurrence of both successive and simultaneous types of pollen mother cell division in *Rauwolfia canescens.*

In the Periplocoideae of the Asclepiadaceae, the simultaneous pollen cell division is predominant just as in Apocynaceae. The resulting tetrads are usually tetrahedral and isobilateral depending on the direction of the second meiotic spindle. In *Hemidesmus indicus* (Nirulla and Richharia, 1945) and *Periploca sepium* (Sax and Husted, 1936), the occurrence of linear tetrads in addition to other types of pollen tetrads has been reported.

In all Cynanchoideae investigated, the pollen mother cells are reported to be of the radially elongated type, as in *Asclepias* (Frye 1901; Gager, 1902; Woodson, 1954, and others). In other genera I have observed the same type in species of *Cynanchum, Matelea, Gonolobus, Stapelia,* and *Sarcostemma,* as well as in *Asclepias, Daemia* (Biswas, 1957) and *Caralluma* (Rao and Rao, 1954). These elongated mother cells undergo two successive meiotic divisions to produce tetrads, which are linear because both of the second meiotic spindles are parallel to the long axis of the pollen mother cells.

In *Secamone* of the Cynanchoideae, the pollen mother cell division is the simultaneous type, agreeing in this respect with that of Apocynaceae and *Periplocoideae,* and sharply contrasting with that of other Cynanchoideae. In the formation of tetrads in *Secamone,* I have mentioned the presence of T-shaped and rhomboidal types, although it might not be impossible to find the linear type as well if more species of this genus were investigated, since this type of tetrad is reported in the primitive subfamily Periplocoideae.

Formation of pollinium sacs in the Cynanchoideae does not necessarily require linear tetrads, although Richharia (1934) postulated

> "that for the organization of pollinium the presence of linear tetrads as has been already said above is necessary and mechanical principles also demand this, hence with some variation here and there, as in *Hemidesmus indicus,* all members belonging to this group, Cynanchoideae, where pollinia are well organized, will exhibit linear tetrads, irrespective of their number of sporangia in each stamen."

In the Apocynaceae the entire surface of the stigma head secretes a more or less sticky substance which in *Apocynum* reaches its maximum organization as five

amorphous bodies ("Teller" of Demeter) alternating with the five anthers (plate 5, fig. 1, and text-fig. 9). In all Asclepiadaceae so far investigated, there are definite regions of the stigma head which actually participate in the secretion of the more highly evolved translators.

In all species of *Secamone* investigated, the entire surface of the stigma head at the level of the translators becomes secretory, although the five grooves within which secretion is limited in more advanced genera are also present (plate 5, fig. 2). The areas of the stigma head opposite the anthers secrete a similar substance which accumulates in the form of five plates between the lobes of each anther. The secretion of the grooves alone is utilized in forming the translators; the superfluous secretion would appear to be solely vestigial. One can hardly avoid the reflection that this situation is reminiscent of an ancestral type which is more like the Apocynaceae.

From morphological studies of certain Asclepiadaceae and Apocynaceae, Demeter (1922) came to the conclusion that from the five-plate type of translator of *Apocynum* the most advanced translators of the Asclepiadaceae might have been derived simply by a "process of folding." In applying this principle, he believed that the shovel and the stalk-adhesive disc portion of a translator of *Periploca graeca* are homologous with the corpusculum and the translator arms of *Asclepias* respectively. Had he studied the ontogeny of the translator of *Secamone*, he would probably have avoided this homology, as we shall see.

In the Apocynaceae, a primitive development of translators can be seen in a very few genera. In the Plumierioideae, generally, the pollen is granular and there is no definite translator formation, although a viscous substance is secreted by the stigma head. Delpino observed in *Lochnera*, a member of this subfamily, that the pollen falls from the anthers upon the upper, non-receptive part of the ring of the stigma head in five heaps. In the subfamily Echitoideae the viscous secretion of the stigma head is retained and in a few genera, such as *Apocynum*, specialization is attained through the secretion of five plates alternating with the five anthers. It is curious to note that in *Apocynum* the pollen tetrads remain together at the time of shedding, due perhaps to a more evolved and specialized tapetum which functions through its secretion as a source of nutrition and perhaps aids in keeping the pollen grains in tetrads as well. To transfer the pollen tetrads by insect pollinators there has been a development of a simple pollinating apparatus in the form of the five plates.

In the Asclepiadaceae one can observe both elaboration and reduction of the pollinating apparatus in different groups. In the most primitive subfamily Periplocoideae, as in *Apocynum*, a tendency of the translators to form a pollen-receiving "shovel" is reached in *Periploca*. Within the same subfamily, the genus *Cryptolepis* is considered to be rather primitive because of the poorly developed translators, a fact which led R. Brown to include it within the Apocynaceae. Falconer (1845) more convincingly separated *Cryptolepis* from the latter and included it within the Asclepiadaceae. In describing the stigma head and the primitive translators Falconer wrote of

> "five straight, shallow, narrow converging furrows, along which are laid as many very delicate, narrow-oblong or linear, bronze-coloured, horny-looking, transparent, membranaceous straps or appendiculae."

He observed that, although the flowers show the characteristics of Apocynaceae

> "yet it is very evident that the plant described above has the whole accessory stigmatic apparatus of the Asclepiadeae . . . . although in a less considerable degree of evolution . . ."

Evidently this type of translator is primitive insofar as the more elaborate shovel or pollen-receiving structure is not yet effected. The pollen tetrads fall onto the sticky ligular part from the adjacent anther lobes at maturity. From this type the more elaborate translator of *Periploca,* perhaps, has been derived through the development of the pollen-receiving structure—a condition which seems to be parallel to the development of similar structures—the five plates of *Apocynum.*

From ontogenetic studies of *Periploca graeca* Demeter (1922), and as I also observed, found that the secretion of a translator follows two different patterns. Thus, in the secretion of the shovel, the substance first produced by the glandular cells of the stigma at that level is a sticky, more or less alveolar substance; this, in a later stage, is followed by another more or less solid secretion. This order of secretion is reversed in the development of the stalk-adhesive disc region.

In *Secamone,* there is nothing equivalent to the shovel of *Periploca,* and the first indication of reduction is evident. It is not surprising to find this structure missing here, since the pollen tetrads are held together in definite pollinium sacs. The pollinium membrane is formed through the secretion of the highly specialized tapetum so characteristic of all Cynanchoideae. This condition certainly does not require a stigmatic adhesive—as in the case of Periplocoideae—to keep the tetrads together.

The secretion of the translators of *Secamone* in reality corresponds to that of *Periploca graeca* and is homologous to the stalk-adhesive disc composition of the latter. The conclusion is based on the ontogenetic studies discussed earlier. In the secretion of the translators of *Secamone,* there is greater emphasis on the solid portion which is larger, relative to the more fluid alveolar part than in the stalk-adhesive disc of *Periploca,* where the reverse is true. In the evolution of the translators, it seems that there has been a greater emphasis on the more solid portion than on the less rigid parts and that this condition has reached its maximum state in the most highly evolved asclepiads.

After having considered the ontogeny of the translators of Periplocoideae and *Secamone,* it is not difficult to correlate similar structures, but on a higher level of evolution, in Cynanchoideae. It is quite clear that the basic parts of a translator in the flowers of the highly evolved asclepiads are the same as in *Secamone,* i.e., a portion which clamps the pollination to insect visitors—the "gland" or more accurately the corpusculum—and a pair of appendages of less rigid substance to which the pollinium sacs are attached—the translator arms. In *Secamone* and members of the Periplocoideae, where only the five vertical, or primary grooves, of the stigma head exist, such a distinction between the translator arms and the corpusculum is not as clear as in *Asclepias,* for example. In the latter, as in other highly evolved

members of Cynanchoideae, one can distinguish two types of secretion of the stigma head: the corpusculum which is secreted by the glandular cells of the vertical grooves, and the two translator arms secreted by two lateral, obliquely descending furrows. Thus, the five areas of the stigma head of *Asclepias* correspond to the secretion of the translators and have the appearance of inverted Y-shaped templates (text-fig. 15). Since the oblique furrows are missing in *Secamone* it would seem that the entire translator apparatus is homologous with the corpusculum of the Cynanchoideae.

The term "corona" has been used variously by asclepiad taxonomists and, in many cases, genera within this family have been differentiated on the basis of the nature of such structures. Woodson (1941) has pointed out the danger in using this term in a very loose sense in the classification of the family. The terminology which he adopted to delimit what is meant by "corona" has the approval of recent authors (Lawrence, 1951); he recognizes three types of corona in the Asclepiadaceae: (1) a faucal annulus derived from the corolla tube, (2) a fleshy radial structure consisting of "various elaborations or enations of the staminal filaments only," (3) sterile appendages of the anthers.

In *Secamone* one may find a combination of all these coronas. In *S. stenophylla,* for example, there are both a staminal and a corolline corona; on the other hand, while in *S. alpinii* the staminal corona is highly developed and there is no corolline corona. In *S. frutescens* the staminal corona is poorly developed—almost lacking—but the apical appendage of the anthers is glandular. The only other species of *Secamone* reported without a staminal corona is *S. astephana.* In describing the latter Choux (1926) writes

> "Les anthères présentent sur leur face dorsale dans le moitié infèrieure deux côtes saillantes formant un triangle à sommet dirigé vers le haut. Mais il n'a sur le dos de ces anthéres aucune trace de couronne. Cet organe fait donc ici entiérement défaut."

The corona of the Apocynaceae is usually of the faucal annulus type; in certain asclepiads this type has been retained; but certain others have been added. It is not impossible that the evolution of corona has followed several lines to produce the most specialized forms met in the Asclepiadaceae. The case of *S. frutescens* might represent a transitional step in the shift of the corona from the corolla tube, which is so predominant in the apocynads, to the stamens, so customary in the majority of the Asclepiadaceae.

Fahn (1953), after an extensive study of many species belonging to 52 families of flowering plants, came to the conclusion that

> "the main phylogenetical trend of the location of the nectary in the flower is acrocentripetal, i.e., a migration of nectariferous tissue from the outer to the inner flower organs . . . ."

Similar conclusions have been drawn by Bonnier (1879), Daumann (1931) and W. Brown (1938).

If one accepts Fahn's notion, one is led to assume, in the case of *S. frutescens,* that the glandular apical appendage of the anthers is a secondarily acquired character and that the staminal corona is vestigial. The lack of a staminal corona in certain highly evolved Asclepiadaceae might support the view that such is a derived

condition. On the other hand, one might argue that the glandular nature of these appendages is a primary character and that the minute corona of *S. frutescens* is not a vestige of a once well-developed organ but rather represents the beginning of evolution of such a structure; the hyaline appendage commonly present in Cynanchoideae would then be construed as derived. In a very few cases, however, these appendages are fleshy, as was reported by Woodson (1941) in *Gonolobus* and *Fischeria*.

Summary

Now that we have discussed several morphological problems in the Asclepiadaceae it may not be amiss to make a few phylogenetic comments. The two closely related families, Apocynaceae and Asclepiadaceae, have been distinguished from one another on the basis of the more specialized pollinia and translators of the latter. Several voices have been raised against this separation: A.-L. de Jussieu, Adanson, and Giseke in the early nineteenth century, Demeter (1922) and others. A. de Candolle (1844) and most contemporary botanists have retained Brown's original separation, while de Candolle hinted that he retained the separation fully aware that the only clear-cut distinction lies in the organization of the pollen. Baillon (1884), although accepting Brown's system, admitted that

> "Les Asclepiadées ont tous les caractères des Apocynées, sauf de leur pollen qui est réuni en masse."

Although there is a large gap between the highly-evolved asclepiads and the most primitive apocynads, the homologies of the most primitive members of the former and the most advanced forms of the latter are unmistakable. It is the degree of development of the pollinating apparatus which separates the two related families. However, this difference is not so striking when one carefully examines the process of pollination in both. One is led almost to believe that this is an orthogenetic evolution.

It has been frequently pointed out that the stigma head of the asclepiad flower differs from that of the apocynads in being more highly specialized and in having definite regions where the translators are secreted. This distinction does not hold true in *Secamone* where the entire surface of the stigma head secretes, although only five poorly-developed grooves contribute to the formation of the translators. Thus, in a member of the highly evolved subfamily Cynanchoideae, one finds a retention of a primitive trait so common in the Apocynaceae. In *Baissea*, an apocynaceous plant, MacFarlane (1933) describes a similar situation in which the five templates of the stigma head are present although the entire organ is glandular. It is quite obvious that the areas of the stigma head opposite the anthers in other Cynanchoideae have lost the ability to secrete during the course of evolution, due perhaps, to the adnation of those organs. In *Secamone* such interruption is avoided since the anthers and the stigma head are not adnate at the level of the translators.

Although the stigma head is not highly evolved in *Secamone*, the organization of pollen tetrads into definite pollinium sacs is a highly-evolved trait. This condition clearly demonstrates that not all of the floral organs advance or retrogress at the same rate or time in the course of evolution.

Although the presence of pollinium sacs in *Secamone* ties this genus with other Cynanchoideae, the type of tetrads and their formation differs markedly from other members of the subfamily. The pollen mother cells in *Secamone* have different configurations depending on their position relative to one another in an anther locule, unlike the elongate prismatic pollen mother cells of other Cynanchoideae. Each pollen mother cell in other Cynanchoideae undergoes two successive meiotic divisions to produce linear tetrads; this is not the case in *Secamone* where these cell divisions are simultaneous, in this respect agreeing with Periplocoideae and Apocynaceae.

The occurrence of the 4-locular anthers of Apocynaceae, Periplocoideae, and *Secamone* certainly presents a primitive character in contrast with the bilocular anthers of Cynanchoideae; *Secamone* does not present a false partition of the sporogenous tissue to simulate the customary 4-locular anthers as was postulated by Demeter (1922), but rather is archetypically 4-locular.

It is a common impression that in all Asclepiadaceae the two carpels are superior at maturity; in Apocynaceae on the other hand there are different degrees of ovary position from superior to essentially inferior (Woodson, 1935). In *Secamone* one frequently finds the carpels more or less subinferior, a situation not otherwise much different from the apocynads.

Phylogenetic classification essentially represents a continuous scale of measurement in which a hierarchy of quantification is as important as in the physical world. Emphasis of dissimilarity is no more important than emphasis on similarity in depicting the course of evolution. Unfortunately, otherwise very competent research would appear to upset the essential balance by the over-emphasis of differences; in other words, "splitting" all too frequently is not compensated by equally appropriate "lumping," with a resulting chaos that may well be more apparent than real. Whether to "lump" or to "split" is a question not to be decided upon the adequacy of our knowledge of a single population, or taxon, but rather upon the adequacy of our knowledge of related populations as well, in order to render both in better perspective as a whole.

In view of the present study, as well as from investigations of others, I am inclined to believe that phylogeny is better portrayed by combining Asclepiadaceae and Apocynaceae into a single family and re-subdividing the group into five subfamilies according to the degree and kind of specialization of the translator apparatus and the relationship between the pollen tetrads to one another at the time of maturity, thus: Plumerioideae, Echitoideae (or Apocynoideae), Periplocoideae, Secamonoideae and Asclepioideae.

Acknowledgment

I would like to express my gratitude to all the persons who assisted me in this work. Dr. Robert E. Woodson, Jr., under whose guidance this research was done, has offered many helpful suggestions and aided me in many ways. To Dean Henry N. Andrews, Jr., and Dr. Robert L. Dressler, I would like to extend my thanks for their encouragement and aid. I also wish to acknowledge the cooperation of the many persons who collected the material used in these studies.

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EXPLANATION OF PLATE

Plate 2

Fig. 1. Longitudinal section of a bud of *Secamone zambesiaca* (X 70).

Fig. 2. Transverse section of a carpel of *S. afzelii* showing the two sterile margins of the placenta (s) (X 300).

Fig. 3. Transverse section of a mature bud of *S. frutescens* showing the 4-locular anthers (X 75).

Fig. 4. Pollinium of *S. alpinii* (glycerin jelly mount) with translator and two of the four pollinium sacs: (X 500), horseshoe-shaped body (a), foamy substance (f), pollinium sac (p).

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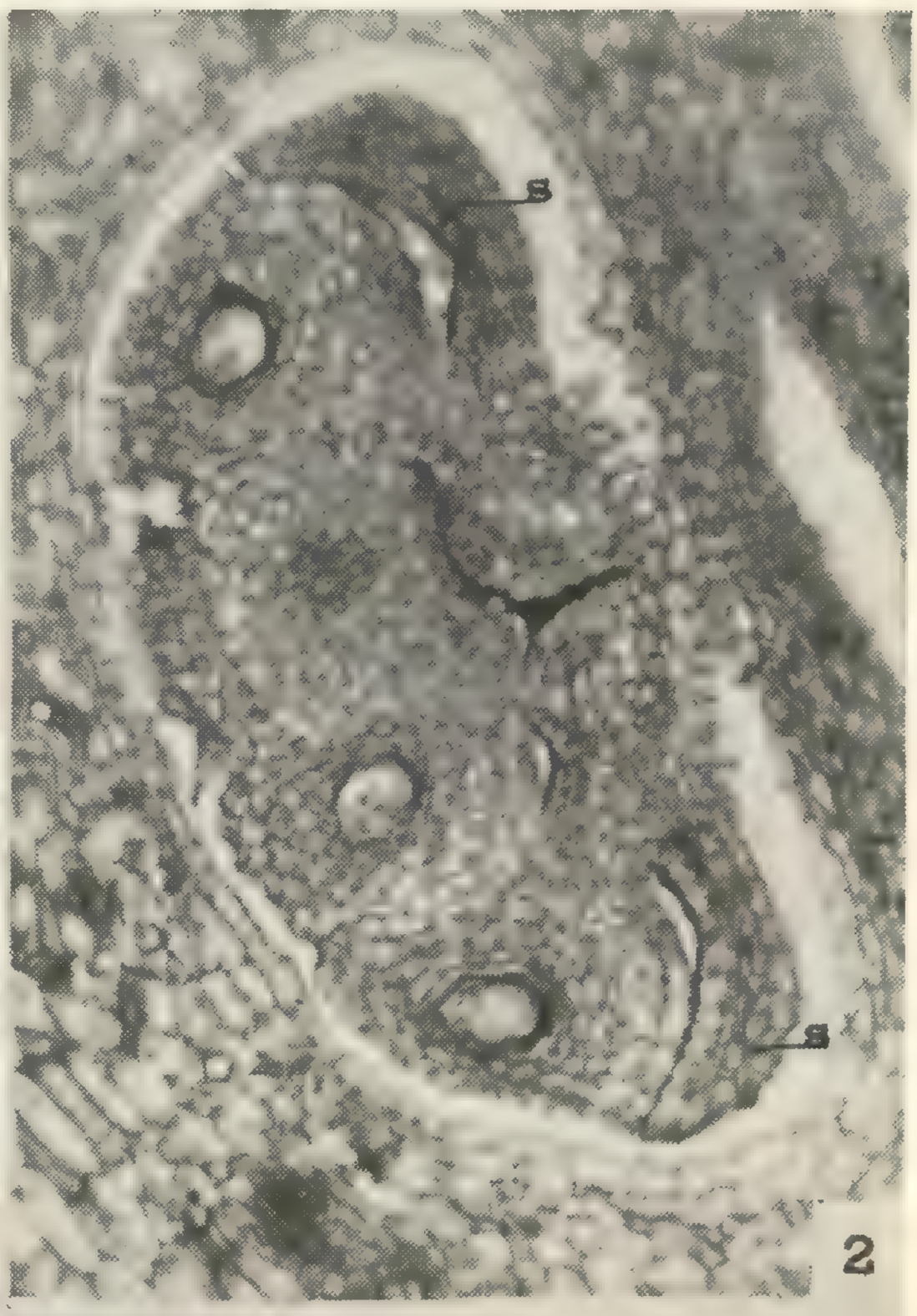

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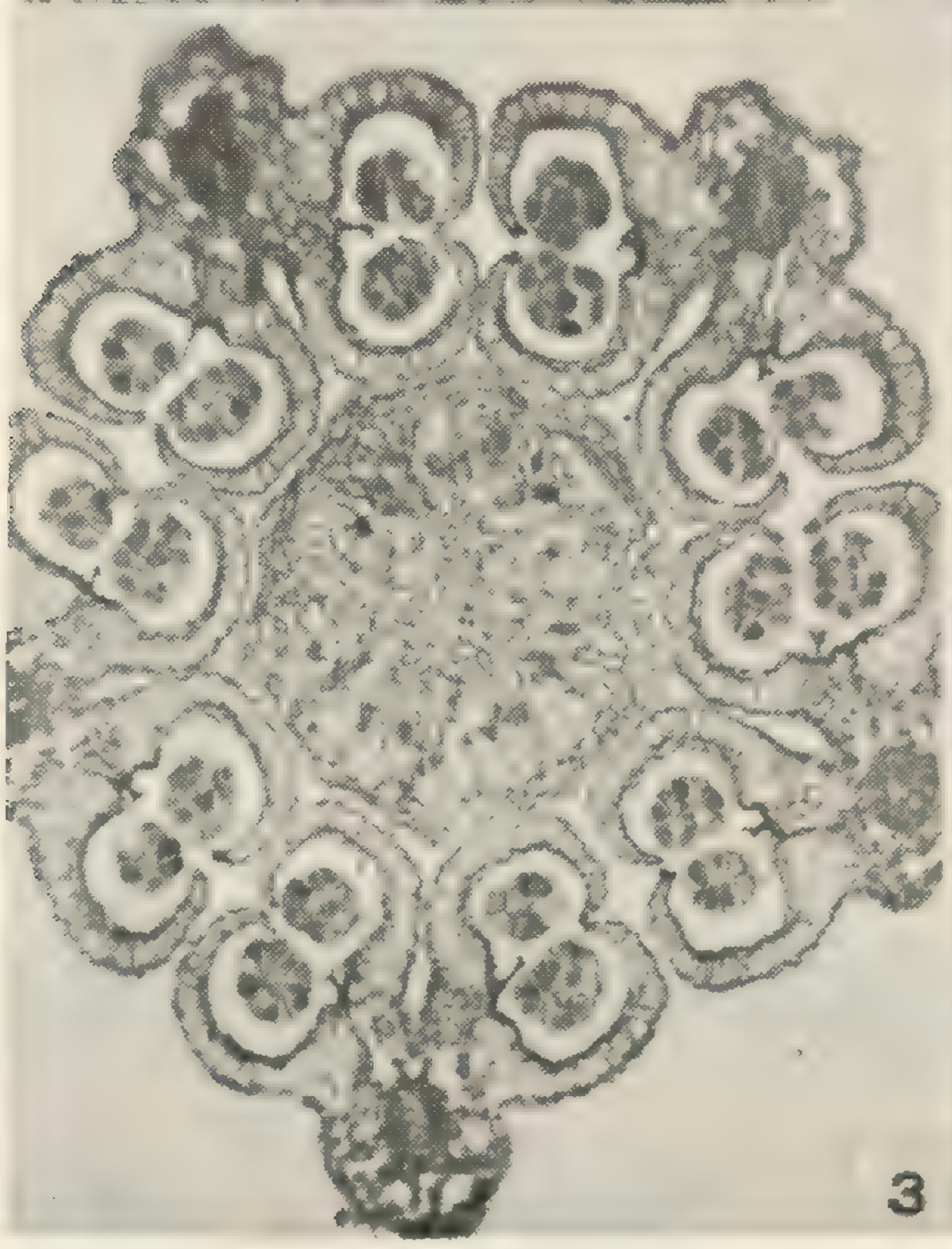

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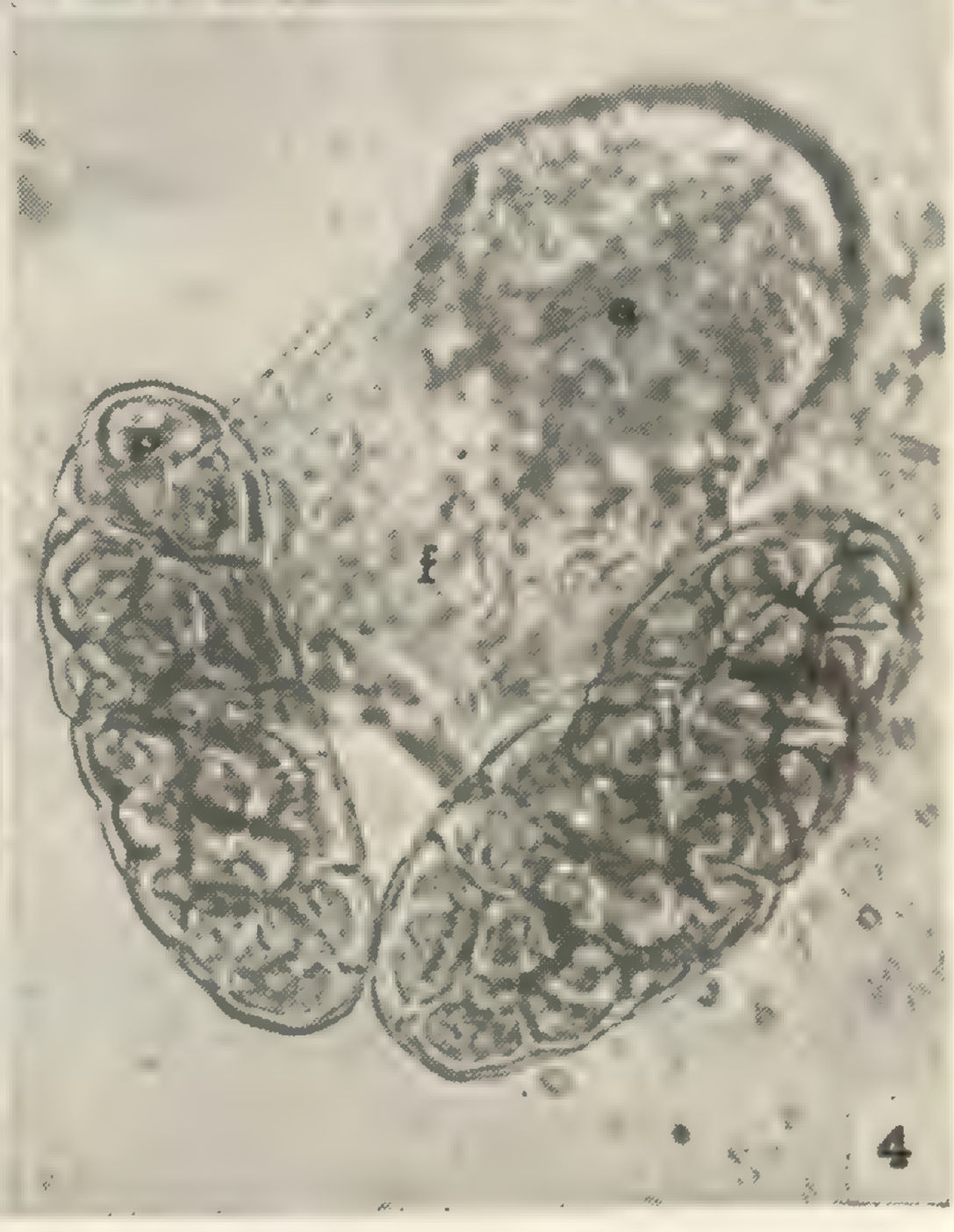

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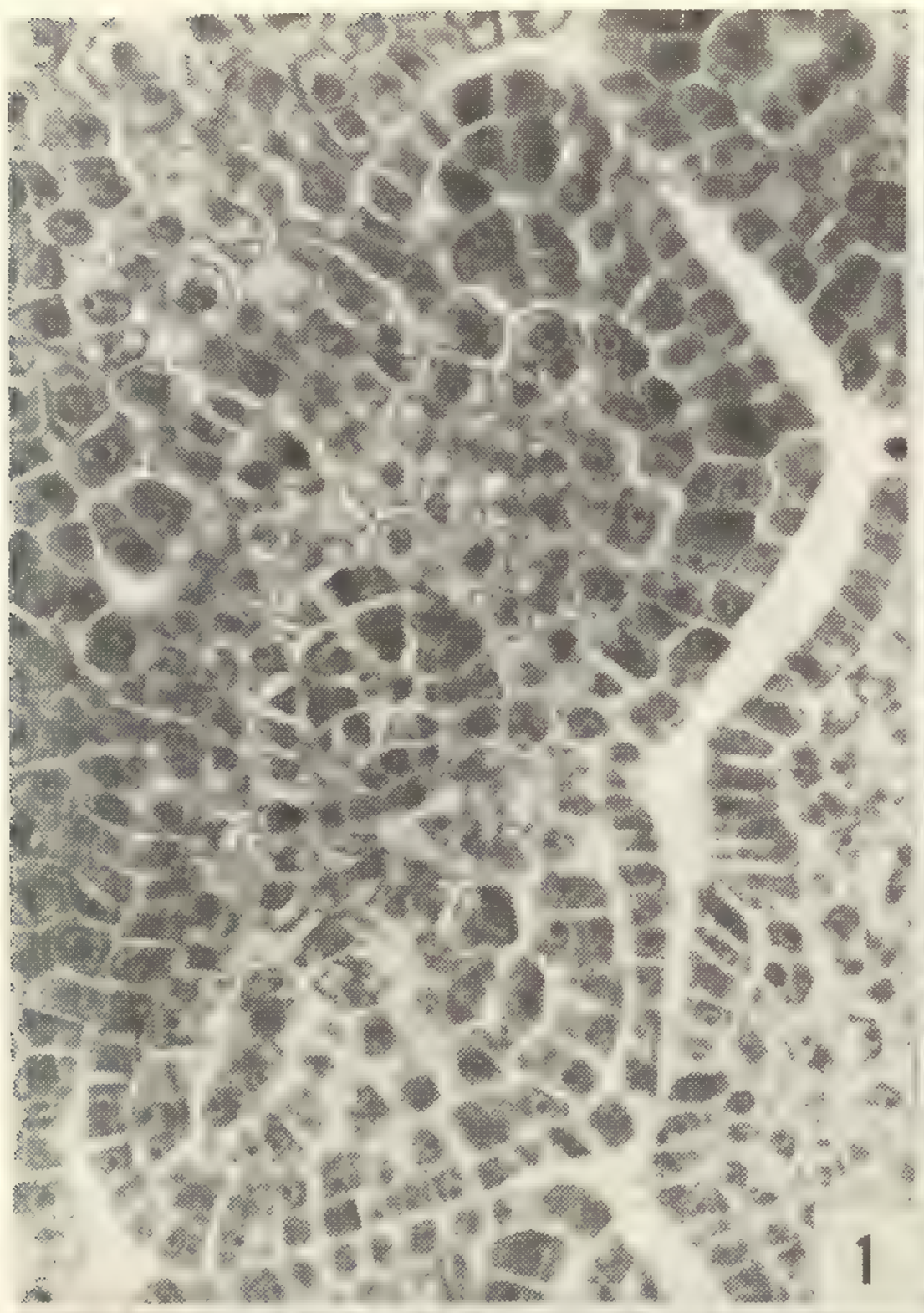
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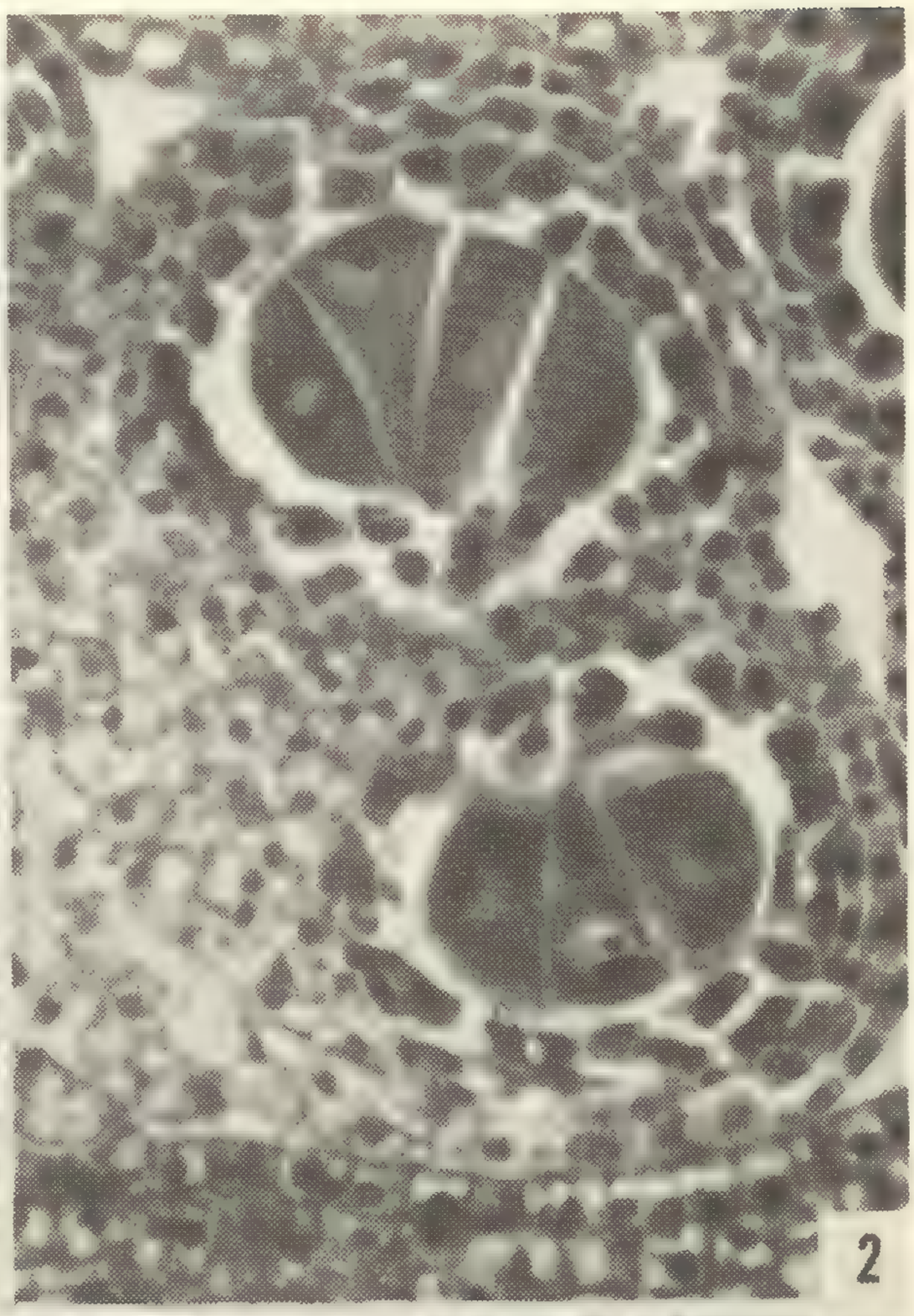
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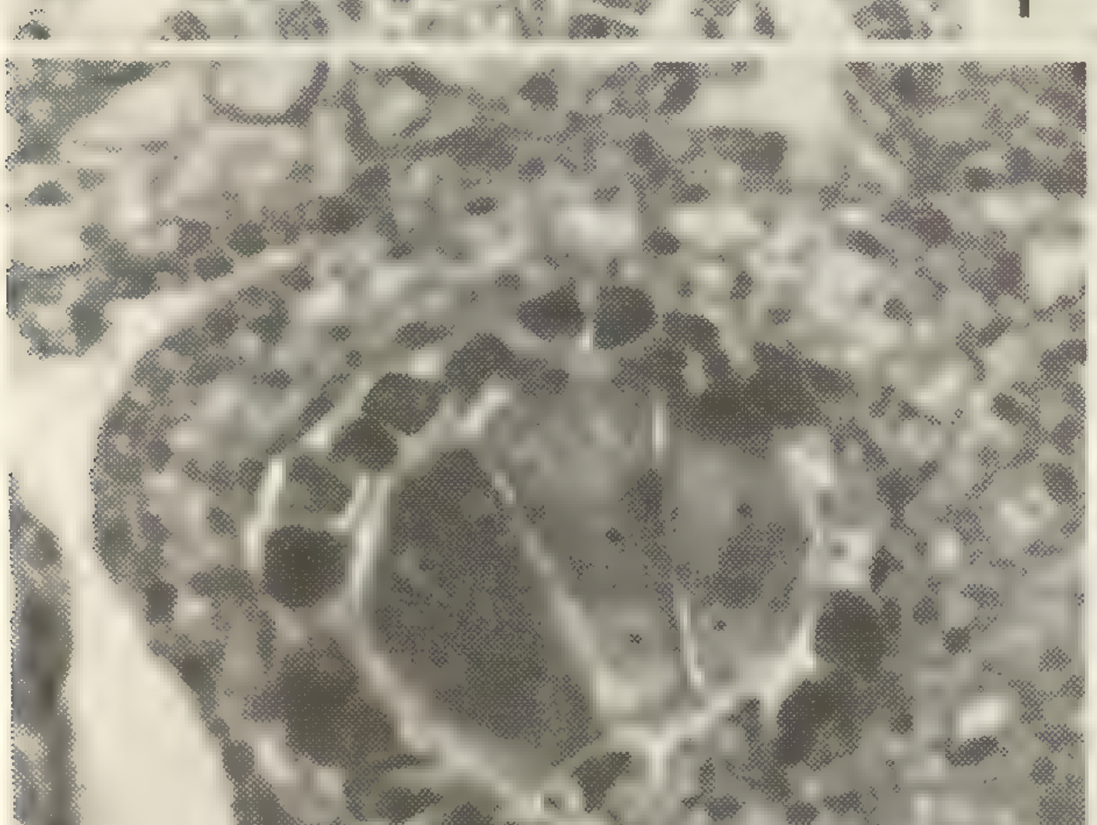
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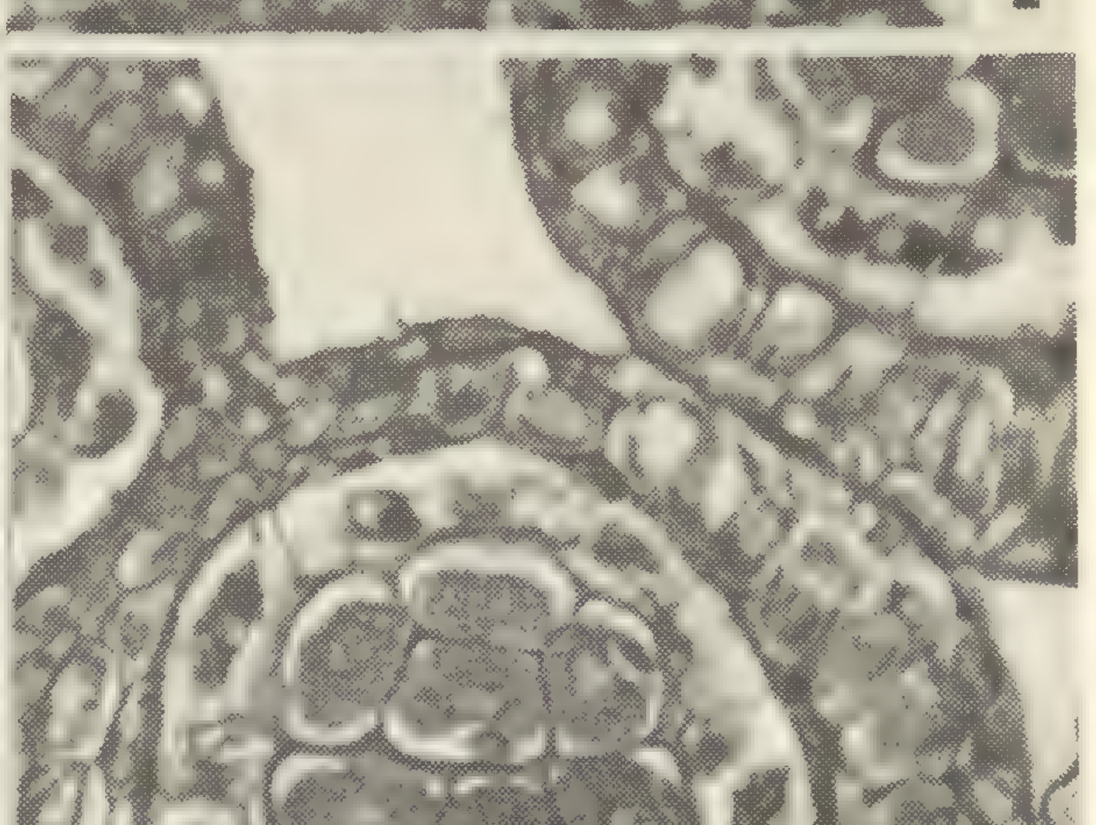

4

Explanation of Plate

Plate 3

Secamone frutescens

Fig. 1. Transverse section of a young anther showing the division of the primary parietal cells (X 600).

Fig. 2. Transverse section of half an anther showing the pollen mother cells (X 500).

Fig. 3. Transverse section of half an anther shortly after the completion of the two simultaneous meiotic divisions (X 520).

Fig. 4. Transverse section of an anther locule showing the rhomboidal and T-shaped tetrads (X 570).

Explanation of Plate

Plate 4

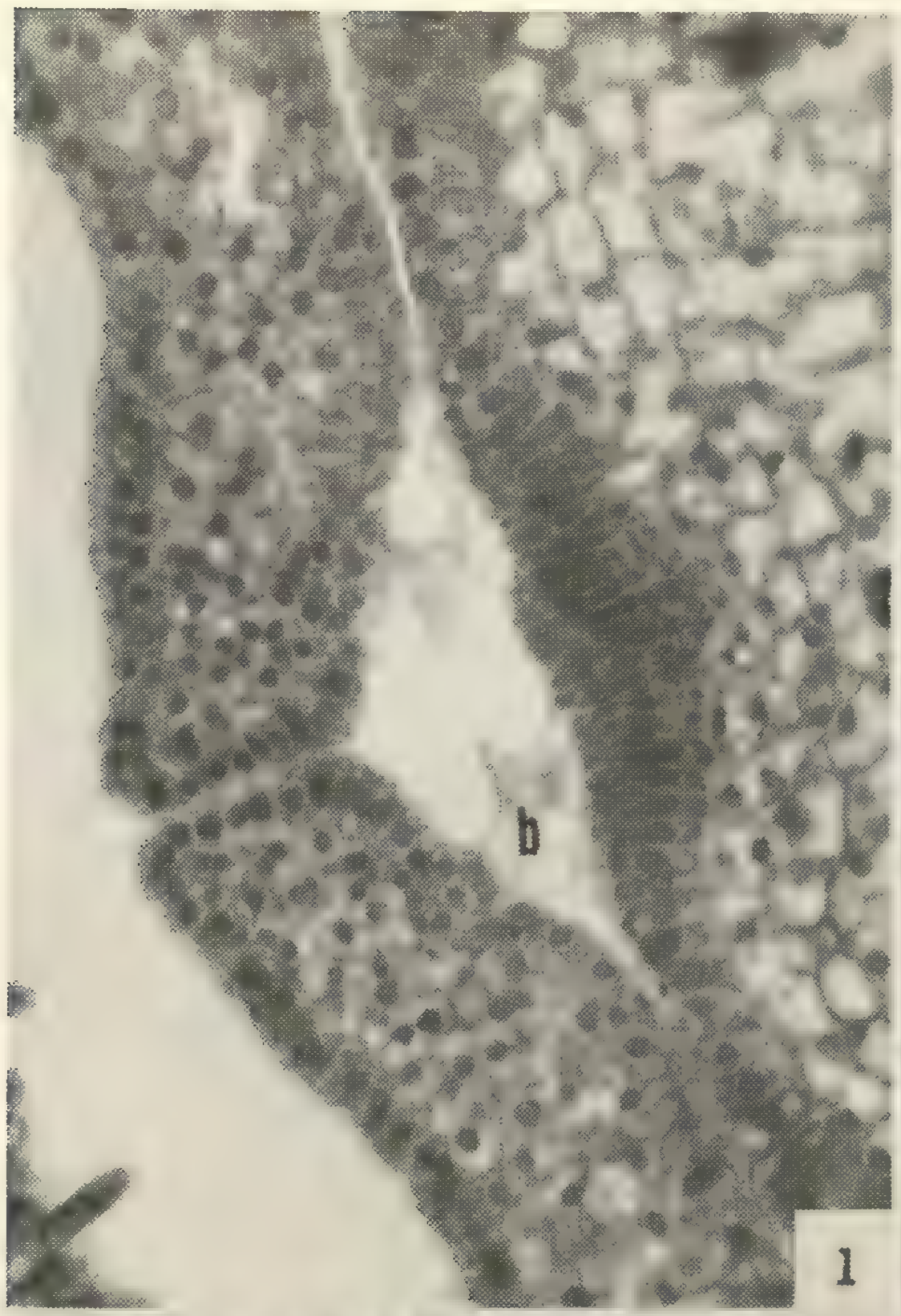
Secamone alpinii

Fig. 1. Transverse section of gynostegium showing an early stage of the secretion of a translator by the stigma head (b), (X 350).

Fig. 2. Later stage in which the horseshoe-shaped body (h) is produced (X 230).

Fig. 3. Longitudinal section of a gynostegium showing the horseshoe-shaped body (a) and the foamy secretion (f), (X 480).

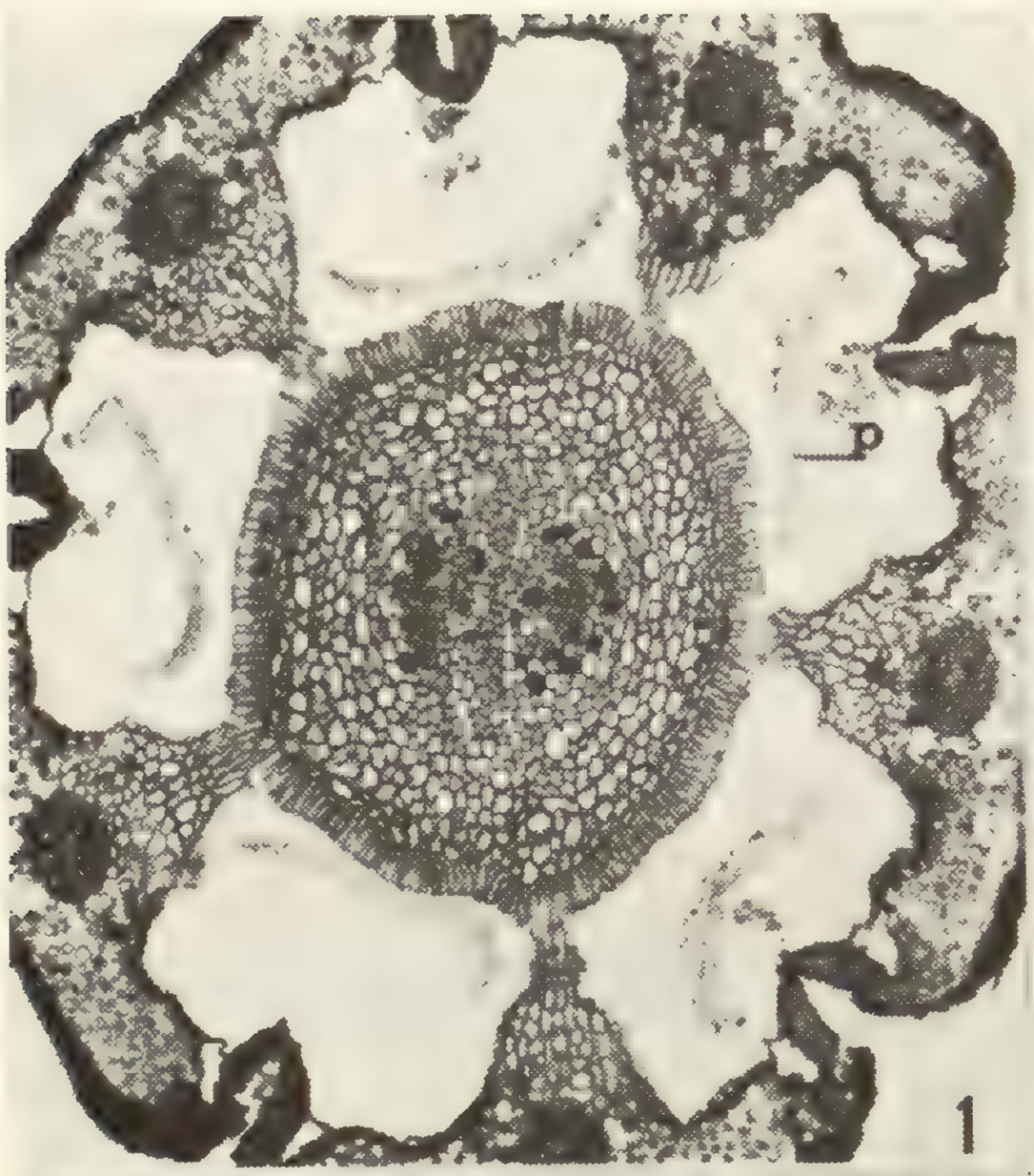
Fig. 4. Transverse section of a mature flower showing the horseshoe-shaped body (a) and a small additional body (p) secreted by the stigma head against an anther (X 350).


b
1

h
2

a
f
3

a
p
4



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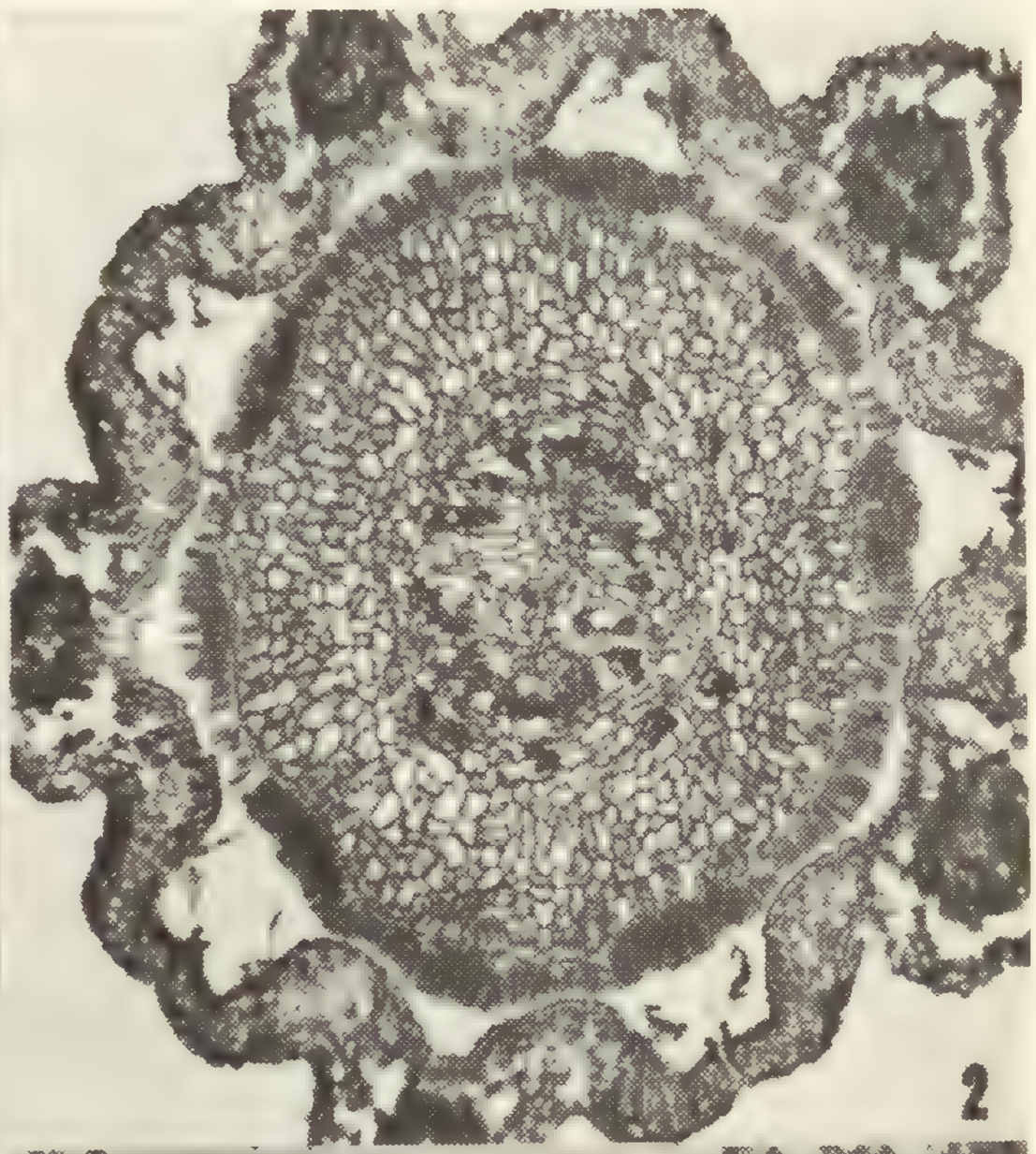

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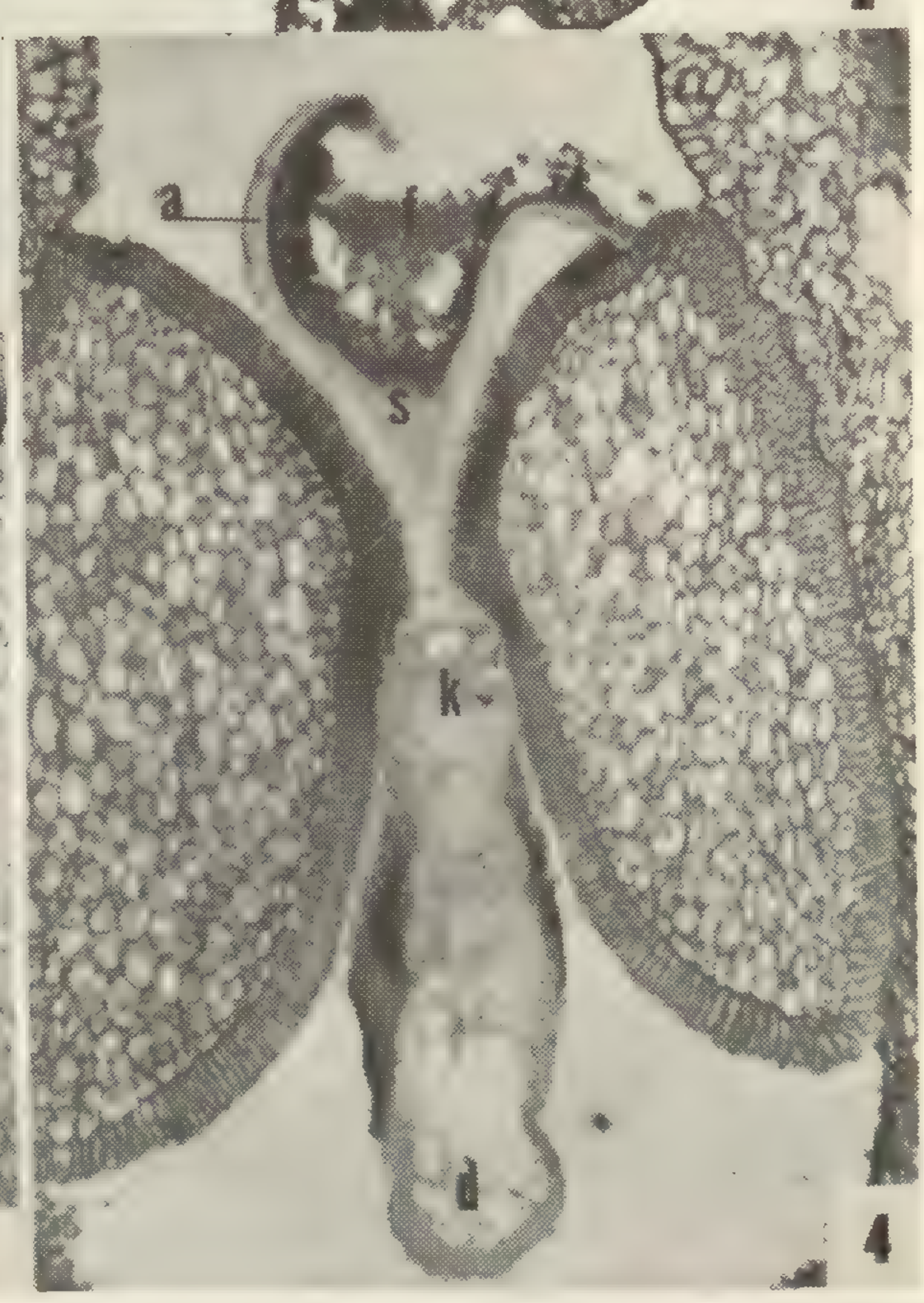


4

Explanation of Plate

Plate 5

Fig. 1. Transverse section of a flower of *Apocynum cannabinum* showing the five small plates (p) alternating with as many stamens (X 85).

Fig. 2. Tranverse section of a flower of *Secamone frutescens* showing the continuously glandular stigma head (x 85).

Fig. 3. Portion of the stigma head of *Periploca graeca* showing the interrupted glandular regions alternating with the anthers (X 75).

Fig. 4. Tangential section of a flower of *P. graeca* showing a pollinium with shovel (s), stalk (k), adhesive disc (d), solid substance (a), foamy secretion (f), (X 90).

Explanation of Plate

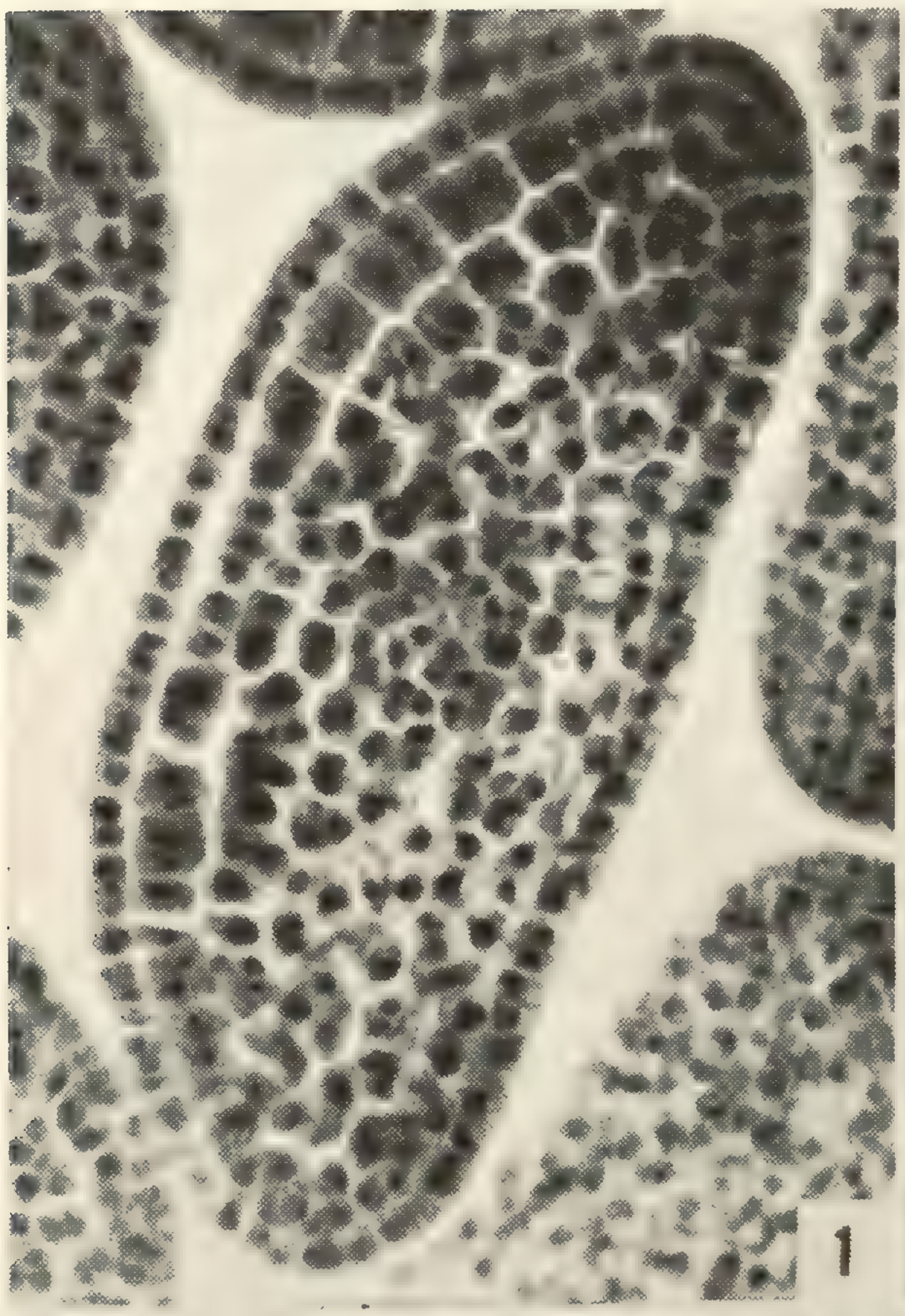
Plate 6

Fig. 1. Transverse section of a young anther of *Matelea quirosii* showing the beginning of divisions within the two hypodermal plates and the origin of the bilocular anther (X 470).

Fig. 2. Tranverse section of an anther of *Asclepias curassavica* showing the outer massive tapetum and the pollen mother cells after the first meiotic division (X 125).

Fig. 3. Transverse section of a young bud of *Vinca rosea* (X 85).

Fig. 4. Transverse section of a bud of *Periploca graeca* showing the massive inner tapetum of the two anther locules of half an anther (X 290).



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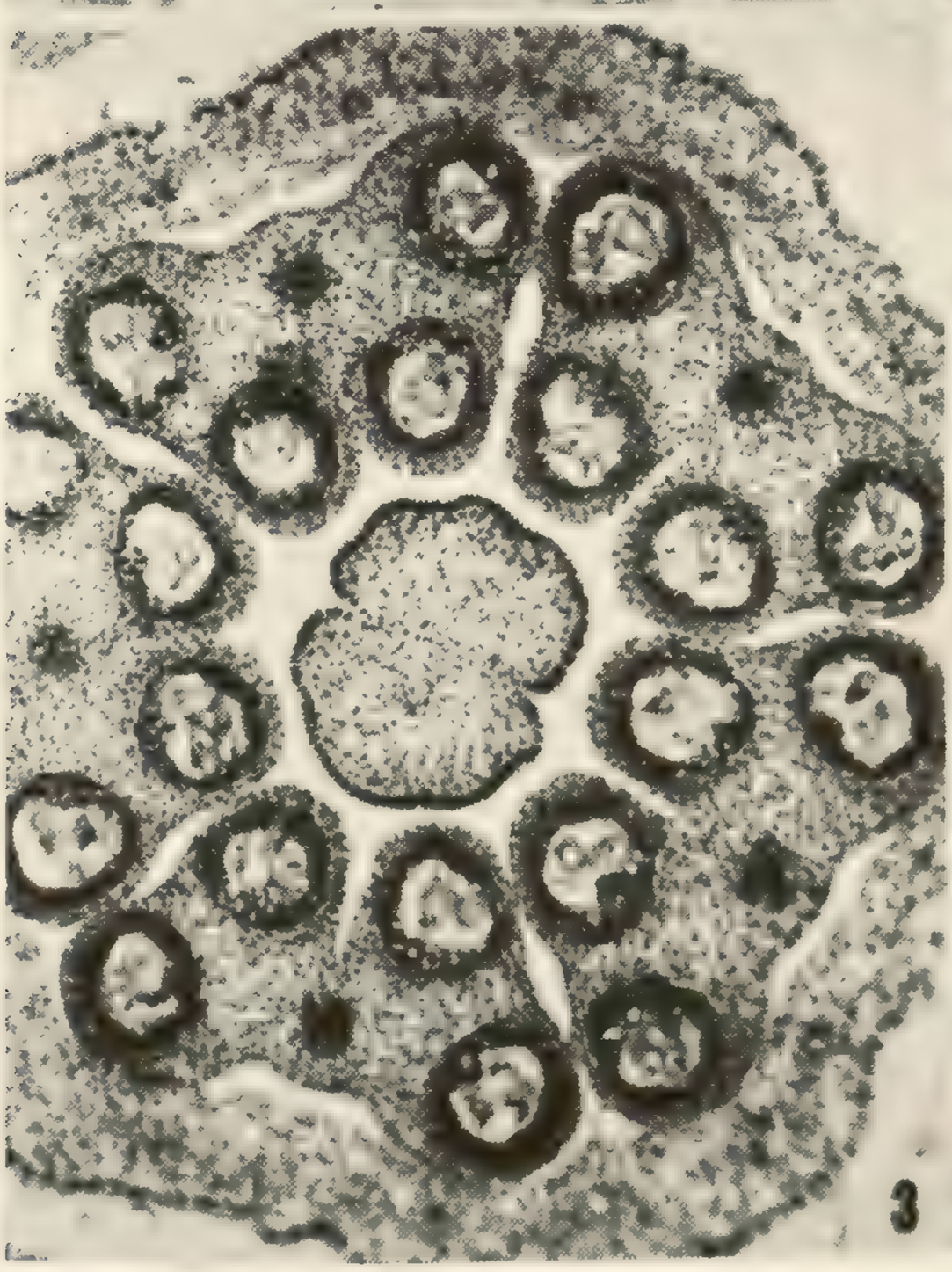

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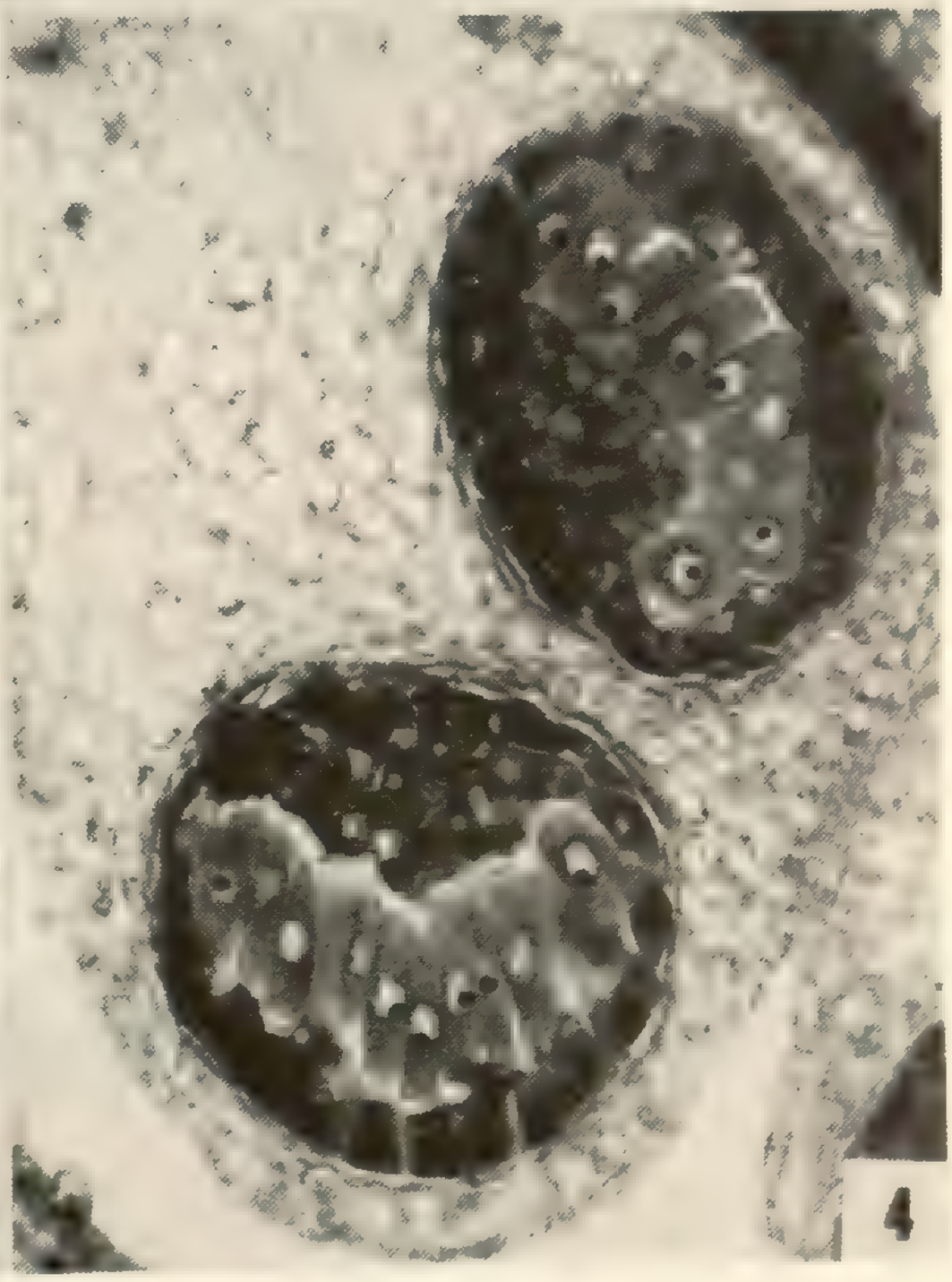

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Appendicula* **dalatensis Guillaumin, Bull. Mus. Hist. Nat. Par. II 32: 562. 1960. Annam (P?).

Appendicula* **inornata Guillaumin, Bull. Mus. Hist. Nat. Par. II 32: 562. 1960. Annam (P?).

Ascochilus **annamensis** Guillaumin, Bull. Mus. Hist. Nat. Paris II 33: 333. Annam (P?).

Broughtonia **negrilensis** Fowlie, Orchid Digest 25: 418. Jamaica (LASCA).

Campylocentrum **schneeanum** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 274. Venezuela (herbarium of the Facultad de Ingeniería Agronómica, Maracay).

Campylocentrum **tyrridion** Garay & Dunsterv., Venezuelan Orchids Illustrated 2: 54. Venezuela (AMES?).

Cattleya **measuresiana** (Warner & Wms.) Blumenschein, Publ. Ci. Inst. Genética São Paulo 2: 26. *Cattleya bicolor* var. *measuresiana* Warner & Wms.

Chaseëlla pseudohydra Summerh., Kirkia 1: 89. Southern Rhodesia (K).

Chaubardia **tigrina** Garay & Dunsterv., Venezuelan Orchids Illustrated 2: 72. Venezuela (AMES?).

Cleisostoma **thomatoglossa** Guillaumin, Bull. Mus. Hist. Nat. Paris II 33: 333. Annam (P?).

Cynorchis **mellitula** Toilliez-Genoud & Bosser, Adansonia 1: 103. Madagascar (P).

Cypripedium macranthum var. **hotei-atsumorianum** Sadovsky, Die Orchidee 12: 63. Japan.

Dactylorchis **russoviii** (Klinge) Löve & Löve, Bot. Not. 114: 38. *Orchis angustifolia* var. *russovii* Klinge.

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Encyclia section **Osmophyta** (Lindley) Dressler, Brittonia 13: 261. *Epidendrum* section *Osmophyta* Lindley.
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Ephemerantha **rhodobalia** (Schltr.) Hunt & Summerh., Taxon 10: 106. *Dendrobium rhodobalion* Schltr.

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Ephemerantha **schinzii** (Rolfe) Hunt & Summerh., Taxon 10: 106. *Dendrobium schinzii* Rolfe.

Ephemerantha schistoglossa (Schltr.) Hunt & Summerh., Taxon 10: 106. *Dendrobium schistoglossum* Schltr.

Ephemerantha **scopa** (Lindley) Hunt & Summerh., Taxon 10: 106. *Dendrobium scopa* Lindley.

Ephemerantha **sematoglossa** (Schltr.) Hunt & Summerh., Taxon 10: 106. *Dendrobium sematoglossum* Schltr.

Ephemerantha **simplicicaulis** (J. J. Sm.) Hunt & Summerh., Taxon 10: 106. *Dendrobium simplicicaule* J. J. Sm.

*Ephemeran*tha **smithii** Hunt & Summerh., Taxon 10: 106. *Dendrobium forcipatum* J. J. Sm., not *Ephemerantha forcipata* (Kraenzlin) Hunt & Summerh.

Ephemerantha **thysanochila** (Schltr.) Hunt & Summerh., Taxon 10: 106. *Dendrobium thysanochilum* Schltr.

Ephemerantha **trifurcata** (Carr) Hunt & Summerh., Taxon 10: 106. *Desmotrichum trifurcatum* Carr.

Ephemerantha **trilamellata** Hunt & Summerh., Taxon 10: 106. *Dendrobium trilamellatum* Schltr., 1911, not *D. trilamellatum* J. J. Sm., 1908.

Ephemerantha **unicornis** (Ames) Hunt & Summerh., Taxon 10: 106. *Dendrobium unicorne* Ames.

Ephemerantha **usterii** (Schltr.) Hunt & Summerh., Taxon 10: 107. *Dendrobium usterii* Schltr.

Ephemerantha **xantholeuca** (Reichb. f.) Hunt & Summerh., Taxon 10: 107. *Dendrobium xantholeucum* Reichb. f.

Ephemerantha xantholeuca var. **obtusiloba** (J. J. Sm.) Hunt & Summerh., Taxon 10: 107. *Dendrobium xantholeucum* var. *obtusilobum* J. J. Sm.

Epidendrum subgenus **Oerstedella** (Reichb. f.) Dressler, Brittonia 13: 264. *Oerstedella* Reichb. f.

Epidendrum **garcianum** Garay & Dunsterv., Venezuelan Orchids Illustrated 2: 122. Venezuela (AMES?).

Epidendrum **rostratum** Garay & Dunsterv., Venezuelan Orchids Illustrated 2: 142. Venezuela, Colombia (AMES?).

Epistephium **hernandii** Garay, Amer. Orchid. Soc. Bull. 30: 498. Colombia (AMES).

Eulophia nuda forma **andersonii** (Hooker f.) Santapau & Kapadia, Jour. Bombay Nat. Hist. Soc. 58: 62. *E. nuda* var. *andersonii* Hooker f.

Eulophia nuda forma **macrantha** (Hooker f.) Santapau & Kapadia, Jour. Bombay Nat. Hist. Soc. 58: 62. *E. nuda* var. *macrantha* Hooker f.

Eulophia nuda forma **purpurea** (Hooker f.) Santapau & Kapadia, Jour. Bombay Nat. Hist. Soc. 58: 62. *E. nuda* var. *purpurea* Hooker f.

Habenaria **nilssonii** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 256. Venezuela (VEN).

Herminium **lanceum** (Thunb, ex Swartz) J. Vuijk, Blumea 11: 228. Ophrys lancea Thunb. ex Swartz.

Koellensteinia **lilijae** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 263. Venezuela (VEN).

Laelia* **briegeri Blumenschein, Publ. Ci. Inst. Genética São Paulo 1: 41. 1960. Brazil.

Laelia* **esalqueana Blumenschein, Publ. Ci. Inst. Genética São Paulo 1: 34. 1960. Brazil.

Laelia* **milleri Blumenschein, Publ. Ci. Inst. Genética São Paulo 1: 38. 1960. Brazil.

Lepanthes **zettleri** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 261. Venezuela (VEN).
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Liparis **tixieri** Guillaumin, Bull. Mus. Hist. Nat. Paris II 33: 434. Annam (P?).
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Malaxis **versicolor** (Lindley) Santapau & Kapadia, Jour. Bombay Nat. Hist. Soc. 58: 347. *Microstylis versicolor* Lindley.
Maxillaria **aristeguietae** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 266. Venezuela (VEN).
Maxillaria **auyantepuiensis** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 269. Venezuela (VEN).
Maxillaria **lasallei** Foldats, Contr. Ocas. Mus. Hist. Nat. Col. "De La Salle" 3: 2. Venezuela (VEN).
Maxillaria **pannieri** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 272. Venezuela (VEN).
Miltonia X *bluntii* forma **lubbersiana** (Reichb. f.) A. D. Hawkes, Na Pua Okika o Hawaii Nei 11: 107. *M.* X *bluntii* var. *lubbersiana* Reichb. f.
Octomeria **cordilabia** C. Schweinf., Bot. Mus. Leafl. 19: 204. Venezuela (NY).
Octomeria **dentifera** C. Schweinf., Bot. Mus. Leafl. 19: 205. Venezuela (AMES).
Octomeria **filifolia** C. Schweinf., Bot. Mus. Leafl. 19: 206. Venezuela (AMES).
Octomeria **flaviflora** C. Schweinf., Bot. Mus. Leafl. 19: 207. Venezuela (AMES).
Octomeria **lancipetala** C. Schweinf. Bot. Mus. Leafl. 19: 210. Venezuela (AMES).
Octomeria **nana** C. Schweinf., Bot. Mus. Leafl. 19: 211. Venezuela (AMES).
Orchis **scopulorum** Summerh., Bol. Soc. Broteriana 35: 55. Madeira (K).
Platystele **ovalifolia** (Focke) Garay & Dunsterv., Venezuelan Orchids Illustrated 2: 268. *Stelis ovalifolia* Focke.
Pleurothallis **nanifolia** Foldats, Bol. Soc. Venez. Ci. Nat. 22: 258. Venezuela (NY).
Pomatocalpa **siamense** (Rolfe ex Downie) Summerh., Orchid Rev. 69: 372. *Cleisostoma siamense* Rolfe ex Downie.
Ponthieva **ovatilabia** C. Schweinf., Bot. Mus. Leafl. 19: 211. Venezuela (AMES).
Sarcanthus **fallax** Guillaumin, Bull. Mus. Hist. Nat. Paris II 33: 334. Annam (P?).
Schomburgkia **wendlandii** (Reichb. f.) H. G. Jones, Amer. Orchid Soc. Bull. 30: 638. *Bletia wendlandii* Reichb. f.
Selenipedium **steyermarkii** Foldats, Bol. Soc. Venez. Cit. Nat. 22: 253. Venezuela (VEN).
Sobralia **speciosa** C. Schweinf., Bot. Mus. Leafl. 19: 198. Venezuela (AMES).
Stelis **latisepala** C. Schweinf., Bot. Mus. Leafl. 19: 199. Venezuela (AMES).
Stelis **obovata** C. Schweinf., Bot. Mus. Leafl. 19: 202. Venezuela (AMES).
Stellilabium **pogonostalix** (Reichb. f.) Garay & Dunsterv., Venezuelan Orchids Illustrated 2: 236. *Telipogon pogonostalix* Reichb. f.
Taeniophyllum **minimum** Guillaumin, Bull. Mus. Hist. Nat. Paris II 33: 435 Annam (P?).
Taeniophyllum **perpusillum** Guillaumin & Tixier, Bull. Mus. Hist. Nat. Paris II 33: 435. Annam (P?).
Xylobium **variegatum** (Ruiz & Pavón) Garay & Dunsterv., Venezuelan Orchids Illustrated 2: 342. *Maxillaria variegata* Ruiz & Pavón.

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Volume XLIX Number 3 and 4

Annals
of the
Missouri Botanical Garden

SEPTEMBER AND NOVEMBER, 1962

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PUBLISHED QUARTERLY BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI

Annals
of the
Missouri Botanical Garden

A quarterly journal containing scientific contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Beginning with Volume 45, 1958:

Subscription Price	$15.00 per volume
Single Numbers	4.00 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., will become sole agent for Annals of the Missouri Botanical Garden. The Agency will handle all subscriptions, all claims (beginning with volume 50 (1963) and all requests for back issues. Out-of-print numbers will be reprinted as may be required.

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FLORA OF PANAMA

BY

ROBERT E. WOODSON, JR.

AND

ROBERT W. SCHERY

AND COLLABORATORS

PART IV

Fascicle 5

NYMPHAEACEAE (J. A. Duke)
CERATOPHYLLACEAE (J. A. Duke)
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ANNALS

OF THE

MISSOURI BOTANICAL GARDEN

Vol. XLIX SEPTEMBER and NOVEMBER, 1962 No. 3-4

FLORA OF PANAMA

Part IV. Fascicle 5*

NYMPHAEACEAE

By J. A. DUKE

Partially or completely submerged rhizomatous aquatics, caulescent or acaulescent, with laticiferous vessels, air spaces and scattered vascular bundles devoid of cambium and vessels, often with idioblasts. Leaves opposite or alternate, the submerged leaves often dissected, the floating leaves more often entire, long-petiolate, often peltate, the venation palmate, with frequent dichotomies or trichotomies, often reticulate. Flowers often large and showy, long-pedicellate, usually solitary, regular, hypogynous to perigynous or epigynous, cyclic to spiral, 3- to 5(-7)-merous. Sepals 3-5(-7), free or slightly connate basally, like or unlike the petals. Petals 3-many, free or slightly connate basally, often brightly colored, occasionally grading into the stamens. Stamens 3-many, the anthers sessile or borne on long, often basally dilated, filaments, entire or apiculate. Carpels 3-many, apocarpous or syncarpous, superior to inferior, with 1-many orthotropous to anatropous ovules attached to the inner wall or pendulous from the summit of the carpel. Fruit a nut, pod or berry, the mature carpels indehiscent, the seeds arillate or naked, smooth or echinate, albuminous or exalbuminous.

A casual perusal of the above description discloses the heterogeneity of this family, a tropical and temperate group of about nine aquatic genera, several of them cultivated. Noting that the characters which hold the family together are largely a function of environmental adaptations while more fundamental characters are quite contrasting, (e.g., inferior vs. superior ovary, cyclic vs. whorled floral arrangement, albuminous vs. exalbuminous seeds, arillate vs. exarillate seeds), Li (in Am. Midl. Nat. 54: 33. 1955) has redistributed the members of Nymphaeaceae *sensu lato* among five families, two of which incur ordinal status as well. Although there is no small amount of logic in Li's disposition, it seems best to retain the Nymphaeaceae *sensu lato* for the Flora of Panama, with only two indigenous genera.

* Assisted by a grant from The National Science Foundation.
Issued May 27, 1963.

a. Leaves all entire or dentate; sepals, petals and carpels numerous; anthers introrse; carpels coalescent, the ovules numerous in each locule; fruit indurate. ..... 1. NYMPHAEA

aa. Some or all of the leaves finely dissected; sepals, petals and usually the carpels 3; anthers extrose; carpels remaining free, the ovules 1-3 in each carpel; fruit baccate ..... 2. CABOMBA

1. NYMPHAEA L.

NYMPHAEA L. Sp. Pl. 510. 1753. partim emend. J. E. Smith in Sibth. & Smith, Fl. Graec. Prodr. 1: 360. 1808-9. nom. conserv.

Castalia Salisb. in Ann. Bot. 2: 71. 1805. nom. rejic.

Rhizomatous, acaulescent, laticiferous, aquatic perennials. Leaves alternate, often polymorphic, long-petiolate; floating leaves ovate to orbicular with a basal sinus; submergent leaves infrequent and emergent leaves rare. Flowers perfect, usually tetramerous, cyclic to spiral, hypogynous to perigynous, often large and showy, white, cyanic or xanthic, floating or emergent on long peduncles arising from the more or less horizontal rhizome; sepals 4(-8), free or slightly connate basally; petals rather numerous, in several series, the inner grading into the stamens; stamens numerous, the outer with petaloid filaments and short broad anthers, the inner with narrower filaments and longer anthers, the anthers all introrse; carpels 3-many, apocarpous to syncarpous, superior or inferior, the carpellary styles radiating from a more or less coalescent disk; ovules numerous, anatropous, pendulous from the inner angles of the carpels. Fruit baccate, mucilaginous, ripening under water, many-seeded, the seeds indurate, operculate, arillate; endosperm scanty, perisperm copious, the embryo minute.

According to Wood (in Journ. Arn. Arb. 40: 98. 1959), the genus contains about 35 species of widespread occurrence (but lacking in New Zealand and the Pacific slope of North America) in quiet, fresh (rarely brackish) waters. After a detailed morphological study of 11 species and two hybrids of *Nymphaea,* Moseley (in Bot. Gaz. 122: 256. 1961) concludes that the arrangement of the floral organs is in transition from spiral to cyclic phyllotaxy, although superficially the carpels, and occasionally other floral parts, appear to be cyclic. For illustrations of some of the Mexican species, the reader is referred to the work of Blackaller (in An. Inst. Biol. Mex. 7: 415. 1937). The genus has not been monographed in entirety since the work of Conard (Carn. Inst. Wash. Publ. 4: 1. 1905). The reader should consult that monograph for some of the synonymic intricacies of the three species found in Panama.

a. Flowers opening by day; carpels free at the sides, the wall between ovary cells being double, the styles short and stout; filaments prominently produced beyond the anthers; leaves coarsely dentate, black-spotted beneath, at least when young ..... 1. N. AMPLA

aa. Flowers opening by night; carpels fused at their sides, the wall between ovary cells being single, the styles long and clavate; filaments scarcely produced beyond the anthers; leaves entire to dentate, pallid or cyanic below.

b. Leaves coarse, sinuate to dentate, usually cyanic below; petioles and peduncles not villose near their apex; sepals conspicuously lineolate ....2. N. RUDGEANA

bb. Leaves thin, entire, pallid below; petioles and pedicels occasionally villose apically; sepals obscurely lineolate ..... 3. N. BLANDA

1. NYMPHAEA AMPLA (Salisb.) DC. Syst. Veg. 2: 54. 1821.

Castalia ampla Salisb. Parad. Lond. 1: *pl. 14.* 1805.

Rhizomatous, aquatic, perennial herbs. Leaves alternate, large and coarse, long-petiolate, the petioles glabrous, the blades suborbicular, sinuate-dentate, green above, purplish and often mottled below, 10-45 cm. long, 10-45 cm. broad, the sinus 5-15 cm. deep; venation coarse, of about 13-29 main veins, these ultimately dichotomizing and trichotomizing and reticulate. Flowers long-pedunculate, usually emersed, opening by day, white, 8-16 cm. broad, the peduncles glabrous; sepals 4, lance-oblong, obtuse to acute, green with purplish striations, 6-10 cm. long; petals several, lance-oblong, obtuse, white, the outermost occasionally yellow-green; stamens numerous, 1-5 cm. long, the outermost longer and broader, the anthers about half as long as the filaments, the filaments conspicuously produced beyond the anthers; carpels ca. 20, laterally connivent, the wall between carpels being double, the styles short, stout and more or less acute, 4-6 mm. long. Fruits 2-3 cm. broad, 1.5-2.5 cm. high, probably maturing under water, pulpy, irregularly dehiscent, many-seeded, the seeds dull gray, operculate, subglobose, ca. 1 mm. broad, slightly longer than broad, strigillose in rows.

Southern Texas and Mexico through the West Indies and Central America to South America. Called "duckweed" by the Barbadians.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey* 652, *Marjorie Brown* 32, 59, *Otis Shattuck* 366, 836, *C. L. Wilson* 39, *Woodworth & Vestal* 562 [annotated by Fassett as var. *speciosa* (Mart. & Zucc.) Casp.]; among the floating islands, north arm of Gigante Bay, *Dodge* 3481; deep water, Gatún Lake, *Killip* 3382; pond west of the Chagres River, opposite Bohío, alt. 20-40 m., *Maxon* 4779; border of lake, Chagres River, at junction of Aguardiente & Quebrada rivers, *Maxon* 6562; between Miraflores and Corozal, alt. 20-30 m., *Pittier* 2204; around Culebra, alt. 50-150 m., *Pittier s. n.*; floating in water, Darién Station, *Standley* 31563. PANAMÁ: swamp between El Jagua Hunting Club on R. Jagua and El Congor Hill, 2 m., *Hunter & Allen* 485.

In addition to the above cited specimens should probably be cited the leaf of *Woodson & Schery* 954 from the vicinity of Madden Lake. The leaf is about 30 cm. long with deeply sinuate-dentate margin, the teeth being as much as 6 mm. long and conspicuously apiculate. Mottling is not evident, but this character is supposed to be constant only in younger leaves. The leaf can be matched perfectly among the other specimens cited for *N. ampla* but the flowers, although a little large, obviously belong to *N. rudgeana*. One might assume that this mixed collection results from collecting the leaf of one species and the flower of another, or from hybridization. The former explanation is probably correct, since the two species involved belong to different subgenera and do not hybridize (see Wood, in Journ. Arn. Arb. 40: 98. 1959).

2. NYMPHAEA RUDGEANA G. F. W. Mey. Prim. Fl. Esseq. 198. 1818.

Castalia rudgeana (G. F. W. Mey.) Britt. & Wils. Sci. Surv. P. R. & Virg. Isl. 5: 305. 1924.

Rhizomatous, aquatic, perennial herbs. Leaves alternate, large and rather coarse, long-petiolate, the petioles glabrous, the blades suborbicular, entire to sinuate-dentate, green above, purple below, 10-30 cm. long, 10-30 cm. broad, the

sinus 2-10 cm. deep; venation prominulous to coarse, of about 7-19 main veins, these ultimately dichotomizing and trichotomizing and reticulate. Flowers long-pedunculate, floating or emersed, opening by night, white, 5-15 cm. broad, the peduncles glabrous; sepals 4, lance-ovate, obtuse to acute, green with purplish striations, 3-7 cm. long; petals several, lance-oblong to obovate, obtuse, white or tinged with yellow; stamens numerous, 1-4 cm. long, the outermost longer and broader, the anthers about half as long as the filaments, the filaments scarcely produced beyond the anthers; carpels ca. 20, laterally connate, the wall between carpels being single, the styles long and clavate, 5-12 mm. long. Fruits 2-3 cm. broad, 1.5-2.5 cm. high, probably maturing under water, pulpy, irregularly dehiscent, many-seeded, the seeds dull gray, operculate, subglobose, ca. 1.6 mm long by 1.2 mm. broad, strigillose in rows.

Central America, West Indies and northeastern South America

CANAL ZONE: floating in edge of canal, Gamboa, *Standley* 28445 (sterile); vicinity of Madden Lake, *Woodson & Schery* 954 (flower only). PANAMÁ: pool in savannah along road between Panama and Chepo; *Dodge, Hunter et al* 16713.

3. NYMPHAEA BLANDA G. F. W. Mey. Prim. Fl. Esseq. 201. 1818.

Castalia blanda (G. F. W. Mey.) Lawson, in Proc. Roy. Soc. Canad. 4: 117. 1888.

Rhizomatous, aquatic, perennial herbs. Leaves radical, mediocre, long-petiolate, the blades subcordate, entire, green above and below, 5-15 cm. long, 3-10 cm. broad, the sinus 1-5 cm. deep; venation delicate, of about 7-13 main veins, the secondaries obscure; petioles glabrous (in Panama) or apically provided with septate hairs. Flowers long-pedunculate, immersed (fide Pittier) to emersed, opening by night, white, 4.0-9.5 cm. broad, the peduncles glabrous or apically provided with septate hairs; sepals 4, lance-ovate, obtuse to acute, green, minutely lineolate, 3-5 cm. long; petals several, lance-oblong to narrowly obovate, white; stamens numerous, 1.0-2.5 cm. long, the outermost longer and broader, the anthers about half as long as the filaments, the filaments scarcely produced beyond the anthers; carpels ca. 20, laterally connate, the wall between carpels being single, the styles obclavate, 5-12 mm. long. Fruits 1.5-2.5 cm. broad, 1-2 cm. high, probably maturing under water, pulpy, irregularly dehiscent, many-seeded, the seeds dull gray, operculate, subglobose, ca. 1.5 mm. long by 1.2 mm. broad, strigillose in rows.

Central America to northeastern South America.

CANAL ZONE: Barro Colorado Island, *Ebinger* 553, *Shattuck* 1153. COCLÉ: pools and their margins in wet llanos between Aguadulce & Antón, ca. 15-50 m., *Woodson, Allen & Seibert* 1225. PANAMÁ: swamps bordering heavy wooded tract along road between Panamá & Chepo, *Dodge, Hunter et al* 16712; water hole at edge of woods near Tapía River, Juan Díaz region, *Maxon & Harvey* 6668; Camino del Boticario, near Chepo, alt. 30-50 m., *Pittier* 4560; Agricultural Experiment Station at Matías Hernández, *Pittier* 6805.

Fassett has proposed, at least on annotation labels, the reduction of *N. fenzliana* and *N. jamesoniana* to forms of *N. blanda*, the typical form of which is characterized by having the petioles and pedicels apically villose and seems to be lacking in the Central American specimens at hand. Fassett's proposal seems

Figure 142. *Nymphaea blanda*

justifiable enough; the specimens cited here as *N. blanda* seem quite homogeneous, although referred by Fassett to two unpublished forms.

2. CABOMBA Aubl.

Cabomba Aubl. Pl. Guian. Fr. 1: 321, *t. 124.* 1775.

Nectris Schreb. Gen. 1: 237. 1789.

Villarsia Neck. Elem. 2: 110. 1790.

Mostly submerged, slender, caulescent and rhizomatous, mucilaginous, aquatic herbs. Leaves monomorphic to polymorphic; submerged leaves opposite or ternate, long-petiolate, the blades dissected into 5-9 trichotomizing or dichotomizing segments, the ultimate divisions more or less linear; floating leaves when present alternate, peltate, bifurcate, linear-elliptic to ovate. Flowers trimerous, perfect, cyclic, hypogynous, solitary on long axillary pedicels, ultimately floating, white to yellow or purple; sepals 3, slightly connate at the base; petals 3, slightly connate at the base, unguiculate, often auriculate; stamens 3-6, the filaments slender, the oblong anthers extrorse; carpels 1-4, free, each with 3 pendulous ovules, the styles longer than the capitate stigmata. Fruiting carpels diverging, each usually with 3 seeds, the seeds elongate, with hygroscopic processes, the embryo surrounded by a small layer of endosperm and a copious perisperm.

As revised by Fassett (in Castanea 18: 116. 1953), this New World genus consists of seven species, of which only the following is known to occur in Panama.

1. Cabomba piauhyensis Gardn. in Hook. Ic. 7: *t. 641.* 1844.

Cabomba pubescens Ule, in Notizbl. 4: 293. 1915.

Cabomba piauhyensis f. *albida* Fassett, in Castanea 18: 123. 1953.

Slender, caulescent, rhizomatous aquatics, the stem villosulous with moniliform hairs, the rufous roots arising adventitiously from the lower nodes. Submerged leaves opposite or rarely ternate, the dissected blades flabellate in outline, 3-7 cm. long, 3-8 cm. broad, with 5-9 freely dichotomizing and trichotomizing divisions, the ultimate segments linear, 0.1-0.3 mm. broad, with weak subparallel venation, the petioles 1-3 cm. long; floating leaves, when present, narrowly to broadly elliptic. Flowers pink, purplish or white, tending toward yellow in the center, solitary on long axillary pedicels; sepals 3, oblong to obovate, obtuse, glabrous, exauriculate and exunguiculate, almost nerveless, 3-8 mm. long, 1-3 mm. broad, scarcely if at all connate; petals 3, narrowly to broadly oblong, obtuse or rounded, unguiculate, laterally auriculate, 3-8 mm. long; stamens 3-6, 2-5 mm. long, the oblong anthers extrorse; carpels (1-)2-3, 2-5 mm. long, separate, arcuate, glabrous to strigillose, mostly 3-ovulate, the style curved to the truncate or capitate stigma. Fruiting carpels banana-shaped, divergent, 1-3-seeded, the seeds ovoid, papillose, 1.5-2.0 mm. long, 1.0-1.5 mm. broad.

Central America and the West Indies south to northern Brazil and Bolivia mostly at low altitudes.

CANAL ZONE: Chagres River, between Gamboa and Madden Dam, *Curry s.n.;* Río Chagres, *Fairchild 2101.* COLÓN: Juan Mina Plantation, Río Chagres, region above Gamboa, alt. 25 m., *Allen 4129.* PANAMÁ: in pool in swamp bordering savannahs & jungles along road between Panamá & Chepo, *Dodge, Hunter et al 16709;* Agricultural Experiment Station at Matías Hernández, *Pittier* 6858.

All specimens here cited have been annotated by Fassett as *C.. piauhyensis. Pittier 6858* has petals more like those illustrated for *C. palaeformis* Fassett, a closely related species with white, scarcely auriculate petals which reportedly ranges only from southern Mexico to Guatemala. Southward from Panama *C. piauhyensis* is replaced by the yellow-flowered *C. australis* Speg.

Figure 143. *Cabomba piauhyensis*

CERATOPHYLLACEAE

By J. A. DUKE

Submerged aquatic herbs devoid of stomata, cuticle and roots, Leaves verticillate, 6-12 at a node, dichotomously dissected, minutely denticulate, often tipped by a pair of bristles. Flowers monoecious, usually solitary at the node, axillary to one of the members of the whorl. Staminate flowers involucrate, lacking a true perianth, the stamens 10-20, extrorse, the anthers 4-locular, the pollen acolpate. Pistillate flowers involucrate, devoid of true perianth, the ovary 1-locular, the style filiform, the stigma lateral, the single ovule orthotropous. Fruit an achene capped by the persistent style and often with other spinescent processes, the seeds exalbuminous, filled with the dicotyledonous embryo devoid of radicle and hypocotyl, the plumule bearing recognizable foliage leaves.

A more or less cosmopolitan family of one genus (*Ceratophyllum*) with four North American species, two of them certainly to be expected in Panama on basis of their distribution, although I am unable to find any reports of the genus having been collected in Panama. In view of the limited distribution of a revision of the North American species by Fassett (in Com. Inst. Trop. Invest. Cientif. 2: 25. 1953) his key is here reproduced:

a. Leaves commonly once or twice forked or rarely simple; marginal teeth on leaf-segments on a broad base of green tissue; fruit not winged, with a terminal spine and 2 basal spines that may be long or much reduced [United States and contiguous Canada; Mexico; Greater Antilles; Guatemala, El Salvador, Honduras; South America] ..... 1. C. DEMERSUM L.

aa. Leaves 2-4 times forked; marginal teeth on leaf-segments with little or no base of green tissue; fruit with a narrow wing and sometimes with marginal spines:

b. Body of fruit 3 mm. or more wide, with marginal spines:

c. Margin of fruit with 8-14 spines mostly 2 mm. or more long; spray of leaves 2-4 cm. in diameter; terminal segments with 3-8 obscure teeth [eastern United States; northeastern Mexico] ....2. C. ECHINATUM A. Gray

cc. Margin of fruit with 16-18 teeth that are mostly less than 1 mm. long; spray of leaves 5-9 cm. in diameter; terminal segments of leaves with 10-20 clearly marked teeth [Guatemala, El Salvador; northeastern South America; Trinidad] ..... 3. C. LLERENAE Fassett

bb. Body of fruit less than 2 mm. wide, without marginal spines [southern peninsular Florida] ..... 4. C. FLORIDANUM Fassett

RANUNCULACEAE

By J. A. DUKE

Perennial or annual herbs with usually opposite, often compound leaves, or lignescent vines with opposite, compound twining leaves; stipules usually absent; petioles not infrequently clasping. Flowers perfect, monoecious or dioecious, actinomorphic or rarely zygomorphic, solitary, racemose or cymose, the floral parts often spirally arranged. Sepals 3-15, separate, imbricate (valvate in *Clematis*), often caducous, the inner often petaloid. Petals as many as or more than the sepals,

occasionally absent and then the sepals petaloid, often with nectariferous glands. Stamens numerous, spirally arranged, separate, hypogynous, the anthers usually 2-celled, introrse, basifixed, longitudinally dehiscent. Carpels 1 to many, separate (connate in *Nigella*), 1-locular, 1-many-ovulate, the ovules anatropous; styles slightly bifid or absent, the stigmata then sessile. Fruit an achene, follicle, or rarely a berry, the seeds albuminous, the embryo small.

A more or less cosmopolitan group, more frequent in temperate and arctic regions, the buttercup family consists of about 30 genera. Although the family contains a few poisonous and medicinal species, its chief economic value is the large number of hardy ornamentals. In highland Central America, species of *Aquilegia, Anemone, Delphinium, Nigella* and *Ranunculus* are cultivated in flower gardens, but only three genera are known to occur naturally in Panama.

a. Lignescent vines climbing by means of foliar tendrils; leaves opposite, compound; flowers dioecious or polygamo-dioecious; achenes with an elongate plumose style ..... 1. CLEMATIS

aa. Herbs; leaves radical or alternate, simple or compound; flowers perfect or polygamous; achenes without a plumose style

b. Leaves with 1-9 leaflets; flowers yellowish; petals present ..... 2. RANUNCULUS

bb. Leaves with many leaflets; flowers greenish or whitish; petals absent ..... 3. THALICTRUM

1. CLEMATIS L.

CLEMATIS L. Sp. Pl. 543. 1753.
Atragene L. l.c. 1753.
Muralta Adans. Fam. 2: 460. 1763.
Viticella Dill. ex Moench, Meth. 296. 1794.
Naravelia DC. Syst. 1: 167. 1818.
Viorna Reichb. Handb. 227. 1837.
Cheiropsis Spach, Hist. Veg. Phan. 7: 260. 1839.
Meclatis Spach, loc. cit. 272. 1839.
Sieboldia Hoffmgg. ex Heynh. Nom. 2: 665. 1846.

Dioecious or polygamo-monoecious, lignescent vines, climbing by means of foliar tendrils (in Central America). Leaves opposite, exstipulate, ternately, pinnately or biternately compound, the leaflets entire to coarsely dentate, often asymmetrical, 1- to 5-plinerved, glabrous to densely sericeous, the rhachis usually pubescent, often twining. Inflorescences of cymes or umbels racemosely disposed along the bracteate, often elongate main axis, unisexual or polygamous; sepals 4-5, valvate, white, greenish or purplish, often petaloid; stamens numerous, separate, the filaments flattened and elongate, the anthers basifixed, 2-celled, longitudinally dehiscent; carpels numerous, separate, the styles comose. Fruit a dry arcuate-ellipsoid achene terminated by the elongate indurate, hirsute style, the ovule pendulous on the dorsal raphe.

Several ornamentals exist in this widespread temperate and tropical genus of both hemispheres. Only the monographer could say how many species there are; the first volume of the Index Kewensis devoted seven and a half columns to the genus. Extreme variability in the leaves, indument and sexuality have resulted

in a rapid increment of named species, many of which, at best, deserve only formal status. The South American species recently have been treated by Lourteig (in Darwiniana 9: 397. 1951, and in Mem. Soc. Cien. Nat. La Salle 16: 19. 1956). Three elements occur in Panama, and I am handling them in the status which I believe would have been assigned them by Lourteig, although the differences between them are by no means constant.

a. Leaflets densely sericeous, coarsely dentate with 2-6 teeth per side, often basally cordate ..... 1. C. HAENKEANA

aa. Leaflets glabrescent, entire or with fewer teeth, basally rounded or truncate ..2. C. DIOICA

1. CLEMATIS HAENKEANA Presl, Rel. Haenk. 2: 69. 1835

Clematis sericea Humb. & Bonpl. ex DC. Syst. 1: 144. 1818, not Michaux 1803.
Clematis grossa Benth. Pl. Hartw. 33. 1840.
Clematis grahami Benth. loc. cit. 5. 1840.
Clematis polycephala Bertol. Fl. Guat. 424. 1840.
Clematis populifolia Turcz. in Bull. Soc. Nat. Mosc. 27: 272. 1854.
Clematis thalictroides Steud. in Flora 39: 407. 1856.
Clematis goudotiana Pl. in Tr. & Pl. in Ann. Sc. Nat. ser. 4. 17: 10. 1862.
Clematis medusae Pl. & Linden, loc. cit. 11. 1862.
Clematis floribunda Tr. & Pl. loc. cit. 9. 1862.
Clematis dioica L. subsp. *sericea* (H. & B. ex DC.) Benoist, in Bull. Soc. Bot. France 87: 124. 1940.
Clematis rhodocarpa Rose, in Contr. U. S. Nat. Herb. 10: 95. 1906.

Dioecious or polygamo-dioecious, perennial, lignescent vines, climbing by means of the foliar tendrils, the branches reddish-brown, striate, often sericeous. Leaves opposite, 3- to 5-foliate, the leaflets sericeous, at least below, often glabrescent, narrowly to broadly ovate, apically acute to acuminate, basally truncate to cordate, coarsely and often asymmetrically dentate with apiculate teeth or lobes, 3-10 cm. long, 2.5-8.0 cm. broad, with 3-9 veins arising palmately at or near the base, the petiolules 1-5 cm. long, the petioles mostly 5-10 cm. long, the sericeous rhachis often coiling. Staminate inflorescences of axillary and terminal compound dichasial cymes, the main axis often elongate and terminating in a simple cyme, giving off 3-7 pairs of simple or compound cymes, the main branches bracteate, sericeous throughout, the bracts progressively reduced; sepals 4, oblong-obovate, apically obtuse; 3-nerved, marginally involute, 6-9 mm. long, 3-4 mm. broad; stamens numerous, 3-7 mm. long, the filaments flattened, the anthers basifixed, 2-celled, 0.6-0.8 mm. long, longitudinally dehiscent, the outer stamens usually longer and perhaps infertile; pistillodes plumose when present. Carpellate inflorescences as the male, the sepals 4, early caducous, 3-ribbed, marginally involute, 6.5-9.0 mm. long, 3-4 mm. broad; carpels numerous, the ovary 1-2 mm. long, arcuate-ellipsoid, pubescent, the plumose style 5-10 mm. long. Mature achenes compressed-ellipsoid, flanged, 2.0-3.5 mm. long, 1-2 mm. broad, reddish-brown, the elongate style plumose with hairs to 4 mm. long.

Mexico through Central America to Argentina, apparently confined to higher elevations in the tropics.

CHIRIQUÍ: vicinity of Cerro Punta, 2000 m., *Allen 1523*. COCLÉ: vicinity of El Valle de Antón, 600 m., *Allen 2062*.

Several colloquial names have evolved for this species in Central America, among the most interesting of which are *barba de viejo, cabello de ángel,* and *bejuco de crispillo,* the latter probably in allusion to the fibrous qualities causing the plant to be used as cordage. The acrid juices of the plant are capable of inducing blisters and find occasional use as a poultice.

2. CLEMATIS DIOICA L. Syst. 10: 1084. 1759.

Clematis americana Mill. Dict. No. 14: 1768.
Clematis brasiliana DC. Syst. 1: 143. 1818.
Clematis glabra DC. loc. cit. 1818.
Clematis caracasana H. & B. ex DC. Syst. 1: 141. 1818.
Clematis havanensis H. & B. ex DC. loc. cit. 152. 1818.
Clematis caripensis HBK. Nov. Gen. & Sp. 5: 36. 1821.
Clematis integra Vell. Fl. Flum. 241. 1825.
Clematis discolor Gardn. in Hook. Jour. Bot. 2: 330, 1843.
Clematis dioica var. α antillensis Eichl. in Mart. Fl. Bras. 13¹: 147. 1864.
Clematis dioica var. *β brasiliana* (DC.) Eichl. loc. cit. 148. 1864.
Clematis dioica var. *americana* (Mill.) O. Ktze. in Verh. Bot. Ver. Brandenb. 26: 103. 1885.

Dioecious or polygamous lignescent vines climbing by means of foliar tendrils, the branches reddish-brown, striate, often pilose. Leaves opposite, with three (or more in var. *brasiliana*) leaflets, glabrate or pilose below, falcate-ovate, entire or with 1 or 2 apiculate teeth, apically acute to long-acuminate, basally rounded to subcordate, 2-8 cm. long, 1.5-5.0 cm. broad, with 3-5 nerves arising near the base, the petiolules 1.0-2.5 cm. long, the petioles to 8 cm. long, glabrous or pilose, the rhachis often coiling. Staminate flowers in axillary and terminal simple or compound dichasial cymes, the pedicels 10-30 mm. long, all branches subtended by progressively reduced bracts, glabrous or pubescent; sepals 4, oblong-obovate, 3-nerved, apically obtuse, marginally involute, 7-11 mm. long, 3.5-5 mm. broad; stamens numerous, the outer longer and perhaps infertile, the anthers basifixed, 2-celled, 0.7-1.0 mm. long, longitudinally dehiscent; filaments flattened; pistillodes plumose when present. Carpellate inflorescences similar to the staminate, the sepals 4, 3-nerved, early-caducous, 6-11 mm. long, 3-5 mm. broad; carpels numerous, ovary 1-2 mm. long, arcuate-ellipsoid, pubescent, the plumose styles 5-10 mm. long. Mature achenes compressed-ellipsoid, flanged, 2.5-4.0 mm. long, 1.0-2.5 mm. broad, reddish-brown, the elongate plumose styles with hairs to 5 mm. long.

Mexico through Central America and the West Indies to southern temperate South America.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, *White & White 107* (var. *brasiliana*); Jaremillo, Boquete District, 4500 ft., *Terry 1279* (var. *brasiliana*); between Hato del Jobo and Cerro Vaca, eastern Chiriquí, alt. 700-1000 m., *Pittier 5424* (var. *brasiliana*). COCLÉ: lower portion of valley and marshes along R. Antón, El Valle de Antón, ca. 500 m., *Hunter & Allen 367* (var. *dioica*).

Figure 144. *Clematis dioica*

As Standley and Steyermark pointed out (in Field Mus. Publ. Bot. 24[4]: 247. 1946,) the two species found in Panama are not clearly differentiated, and this obscurity of definition is carried down to the varietal level also; so it is only with reluctance that I refer the specimens of *C. dioica* to variety. The stems of the plant are used as cordage, the sap as a glue, and the seed pods as a kapok.

2. RANUNCULUS L.

RANUNCULUS L. Sp. Pl. 548. 1753.

Ficaria Huds. Fl. Angl. 1: 213. 1762.
Hecatonia Lour. Fl. Cochinch. 1: 302. 1790.
Ceratocephala Moench, Meth. 218. 1794.
Krapfia DC. Syst. 1: 228. 1818.
Batrachium (DC.) S. F. Gray, Nat. Arr. Brit. Pl. 2: 720. 1821.
Casalea St. Hil. Fl. Bras. Mer. 1: 6, *pl. 1*. 1824.
Aphanostemma St. Hil. loc. cit. 10. 1824.
Oxygraphis Bunge, Verz. Suppl. Alt. 46. 1836.
Cyrtorhyncha Nutt. ex T. & G. Fl. N. Am. 1: 26. 1838.

Flammula Dod. ex Fourr. in Ann. Soc. Linn. Lyon 2[16]: 324. 1868.
Coptidium Nyman, Consp. 13. 1878.
Kumlienia Greene, in Bull. Cal. Acad. 1: 337. 1886.
Arcteranthis Greene, in Pittonia 3: 190. 1897.
Beckwithia Jepson, in Erythea 6: 97. 1898.
Halerpestes Greene, in Pittonia 4: 207. 1900.
Rhopalopodium Ulbrich, in Notizbl. 8: 253. 1922.
Aspidophyllum Ulbrich, loc. cit. 268. 1922.

Glabrous to pubescent erect or procumbent herbaceous annuals or perennials, the stems occasionally rooting at the nodes, the roots fibrous, fascicled. Leaves radical or cauline, exstipulate, entire, dissected or compound, alternate or rarely opposite, glabrous to pubescent, often with acrid juice. Inflorescence terminal, the flowers perfect; sepals 5(-3-6), imbricate, caducous; petals (0-)5(-26), yellow, white or red, separate, with a nectariferous pit at the base, unguiculate; stamens commonly 10, often more, rarely fewer; anthers 2-celled, basifixed, longitudinally dehiscent; carpels 5-many, the single ovule attached near the base of the cell. Achenes capped by the elongate style, glabrous or hairy, smooth or variously ornate.

Comprised of about 250 species in temperate and subarctic regions of both hemispheres, the buttercup genus is represented in Central America by few species, most of them confined to moderately high elevations. In his recent monograph of the North American species, Benson (in Am. Midl. Nat. 40: 1. 1948, and 52: 328. 1954) treats about 100 species. A few species with large petals are cultivated as ornamentals. Two species are reported from Panama.

a. Achenes 20-25, the beak ca. 1 mm. long, recurved; petals 5, at least half as broad as long; stems rooting at the lower nodes; roots ca. 0.5 mm. in diameter ..... 1. R. REPENS

aa. Achenes 10-20, the beak 1.5-2.7 mm. long, straight; petals 5-10, more than twice as long as broad; stems not rooting at the lower nodes; roots 1-3 mm. in diameter ..... 2. R. PILOSUS

1. RANUNCULUS REPENS L. Sp. Pl. 554. 1753.

Ranunculus intermedius Eat. Man. Bot. 3: 1822.
Ranunculus repens α *glabratus* DC. Prodr. 1: 38. 1824.
Ranunculus clintonii Beck, Bot. N. & Mid. States 9. 1833.
Ranunculus repens var. *pleniflorus* Fernald, in Rhodora 19: 138. 1917.

Hirsute, prostrate to ascending perennials to 80 cm. tall, rooting at the lower nodes, the roots filiform. Cauline leaves alternate, hirsute, often glabrescent, the blades trifoliate, the leaflets often deeply 3-lobed and dentate, rhombic-deltoid, apically acute and apiculate, basally obtuse to acute, 2-4 cm. long, 1.5-3.0 cm. broad, the central petiolules 0.5-4.0 cm. long; petioles 1-20 cm. long, the swollen leaf base to 2.5 cm. long; radical leaves similar to the cauline but often with larger blades and longer petioles. Flowers mostly solitary in the upper axils, the pedicels 2-10 cm. long; sepals 5, greenish, 3-nerved, 4-7 mm. long, 2-4 mm. broad, caducous; petals 5, yellow, occasionally drying white, ellipsoid, obtuse, 5-13 mm. long, 3.5-10.0 mm. broad, the nectary flap semicircular, glabrous, ca. 0.5 mm. long, (1.0-1.3 mm. fide Benson); stamens numerous, 2-3 mm. long, the anthers about as long as the filaments; carpels numerous. Fruiting heads subglobose, 6.0-7.5 mm.

long; achenes 20-25, subdiscoid, puncticulate, ca. 2.5 mm. long, 2.0-2.5 mm. broad, the beak ca. 1 mm. long, strongly recurved; fruiting pedicels 4-15 cm. long, the receptacle ca. 3 mm. long, pubescent.

Presumably a native of Europe, but widely occurring in both North and South America.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, 6000 ft., *Davidson 444;* valley of the upper R. Chiriquí Viejo, vicinity of Monte Lirio, 1300-1900 m., *Seibert 159;* vicinity of Bajo Chorro, 1900 m., *Woodson & Schery 646.*

A Gray Herbarium duplicate of *Woodson & Schery* 646 was determined by Benson as *R. repens.* The duplicate in the herbarium of the Missouri Botanical Garden departs from Benson's description of *R. repens* in having unusually small floral parts and fewer carpels and stamens.

2. RANUNCULUS PILOSUS HBK. ex DC. Syst. 1: 287. 1818.

Ranunculus amarillo Bertol. Fl. Guat. 24. 1840.

Hirsute ascending perennials to as much as 70 cm., not rooting at the nodes, the roots fibrous. Cauline leaves alternate, appressed-hirsute, gradually reduced to linear bracts, the blades trifoliate, the leaflets often lobate and dentate, deltoid to rhombic, apically acute, basally attenuate to rounded, 2-10 cm. long, 1-8 cm. broad, the central petiolules to 4 cm. long; petioles 1-10 cm. long, the sheaths mostly 5-15 mm. long; radical leaves similar to the cauline but often with larger blades and longer petioles. Flowers 1-several in terminal lax racemes, the pedicels 2-12 cm. long; sepals 5, greenish-yellow, 5- to 7-nerved, dorsally hirsute, 5-7 mm. long, 2.5-4.0 mm. broad, promptly caducous; petals 5-10, yellow, occasionally drying white, narrowly obovate, broadest above the middle, 8-12 mm. long, 3-5 mm. broad, the nectary flap reniform to semicircular, ca. 1 mm. long; stamens numerous, becoming 4 mm. long, the anthers ca. 1 mm. long; carpels numerous. Fruiting heads subglobose, 7-8 mm. long; achenes 10-20, ellipsoid to discoid, 2.5-3.0 mm. long, 2-3 mm. broad, the beaks 1.5-3.0 mm. long, arcuate; fruiting pedicels 4-15 cm. long, the receptacles 2.5-3.5 mm. long, hispid.

Paludal areas, 4000-8000 ft., Mexico to Panama.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, 6000 ft., *Davidson 444* (GH, fide Benson).

Davidson 444 in the herbarium of the Missouri Botanical Garden is *Ranunculus repens* as determined by Benson.

3. THALICTRUM L.

THALICTRUM L. Sp. Pl. 545. 1753.
Physocarpum Bercht. & Presl, Rostl. 1: 14. 1823.
Ruprechtia Opiz, Seznam 86. 1852, nec C. A. Mey. nec Rchb.
Sumnera Nieuwl. in Am. Midl. Nat. 3: 254. 1914.
Leucocoma (Greene) Nieuwl. loc. cit. 3; 1914.

Glabrous to pubescent erect herbaceous or lignescent perennials, occasionally stoloniferous, the roots mostly fibrous, occasionally tuberous. Leaves radical and

Figure 145. *Ranunculus pilosus*

cauline, the cauline usually alternate, decompound, glabrous to pubescent, with swollen petiolar sheaths. Inflorescences mostly terminal, paniculate or rarely racemose or subcorymbose, bracteate or ebracteate, the flowers perfect, dioecious or polygamous; sepals 4-5(-7), caducous, greenish or petaloid; petals absent; stamens numerous, free, the anthers basifixed, often apiculate; carpels few to many, indehiscent, uniovulate. Achenes few to numerous, more or less saccate, often costate or nerved, the elongate styles frequently deciduous.

Thalictrum is most common in temperate portions of the northern hemisphere, where a few species are handsome enough to be cultivated. In a monograph of the American *Thalictra* and their Old World allies, Boivin (in Rhodora 46: 337. 1944.) treated 112 species and varieties. Only two species are reported from Panama.

a. Plants not glaucous, glabrous; carpels 3.0-3.2 mm. broad .....1. T. VIRIDULUM
aa. Plants glaucous, pubescent with capitate hairs; carpels 2.0-2.2 mm. broad .....2. T. PANAMENSE

1. THALICTRUM VIRIDULUM Boivin, in Rhodora 46: 406. 1944.

Verdant glabrous perennials to 1.5 m. high, the lignescent twigs sulcate. Cauline leaves alternate, glabrous, the blades 3- to 4-times pinnately compound, the pinnae opposite, the ultimate segments mostly 3-lobed, ovate or obovate to reniform or obreniform in outline, often asymmetrical, apically rounded, basally truncate to cordate, 10-22 mm. long, 10-25 mm. broad, the petiolules 5-25 mm. long. Flowers polygamo-monoecious, mostly perfect, some strictly staminate, paniculate, with linear bracts 2-15 mm. long; sepals 4-5, ovate, apically rounded, 5-nerved, 3-4 mm. long, 2.0-2.5 mm. broad, greenish; stamens numerous, pinkish, the filaments 0.5-1.0 mm. long, the anthers basifixed, 1.5-3.0 mm. long; carpels few, pinkish, the body about 1 mm. long, the style 7-10 mm. long, deciduous. Achenes ca. 4.5 mm. long, 3.0-3.5 mm. broad, granular, with a stipe and an apiculum each about 1 mm. long, 3-ribbed, the ribs occasionally branching and anastomosing.

Known only from the type locality.

CHIRIQUÍ: in rocky gorge of river, valley of the upper R. Chiriquí Viejo, vicinity of Monte Lirio, 1300-1900 m., *Seibert 204*.

Boivin's description of this species, based on *Seibert 204* at the New York Botanical Garden, says of the leaves "perfecte 5-ternata." On the specimen at hand, there is no swollen leaf base, so I cannot be sure whether I have a leaf or a leaflet, but it is 3- to 4-times decompound, with only the ultimate divisions ternate, all others being pinnate.

2. THALICTRUM PANAMENSE Standley, in Field Mus. Publ. Bot. 22: 19. 1940.

Glaucous capitate-pubescent perennials to as much as 1.3 m. high, the lignescent twigs shallowly canaliculate. Cauline leaves alternate, capitate-pubescent, the blades 3- to 4-times pinnately compound, the pinnae opposite, the ultimate divisions often ternate or 3-lobed, often asymmetrical, ovate to reniform in outline, apically rounded, basally truncate to cordate, 5-12 mm. long, 5-12 mm. broad, the petiolules 2-8 mm. long. Flowers few, the inflorescence less than 3.5 cm. long, ap-

Figure 146. *Thalictrum viridulum*

parently unisexual; sepals (3-)4, ovate, obtuse, 3-nerved, 2.0-2.5 mm. long, ca. 1 mm. broad, promptly caducous; carpels few, the body about 1 mm. long, the style ca. 2 mm. long. Achenes 3.5-4.5 mm. long, 2.0-2.3 mm. broad, glandular-puberulent, stipitate, 3-ribbed, the ribs rarely branching or anastomosing; fruiting pedicels to 15 mm. long.

Known only from the type locality.

CHIRIQUÍ: savannahs, Boquete District, 4500 ft., *Davidson 791*.

BERBERIDACEAE

By J. A. DUKE

Perennial herbs, shrubs or small trees, often rhizomatous, occasionally armed. Leaves alternate, radical or crowded at the ends of spur branches, stipulate or exstipulate, simple, binate, trifoliate or pinnate, membranaceous and deciduous to coriaceous and evergreen. Flowers bisexual, cyclic, actinomorphic, solitary, racemose, spicate or paniculate, the perianth imbricate, usually multiseriate, the outermost whorl often grading into bracteoles (prophylls). Perianth whorls mostly trimerous, occasionally dimerous or pentamerous, often yellow, the segments usually free. Stamens usually in two whorls, hypogynous, the anthers usually bilocular and valvate (occasionally longitudinally dehiscent). Carpels usually solitary, uni- to pluriovulate, the placentation parietal or basal, the styles and stigmata usually simple. Fruit a berry, capsule or rarely an achene, the seeds anatropous, occasionally arillate, albuminous, the embryo straight and small.

A small family of about ten genera and 500 species, mostly of north-temperate latitudes, the Berberidaceae are represented among Panamanian collections solely by *Berberis nigricans* from Chiriquí. Species of the genera *Mahonia, Berberis* and *Nandina* are cultivated in temperate regions and might appear in upland gardens of Central America. *Mahonia paniculata,* with imparipinnate leaves with 7-8 pairs of spinulose-serrate leaflets and with broad paniculate inflorescences, has been collected on some Costa Rican volcanoes, and might be expected in upland Chiriquí.

1. BERBERIS L.

Berberis L. Sp. Pl. 330. 1753.

Small, often profusely branched shrubs, occasionally armed with 1- to many-pronged barbs. Leaves simple, often crowded toward the apex of spur branches, membranaceous to coriaceous, deciduous or evergreen, sessile or with a short alate petiole, entire, revolute, or spinose-serrulate, subenervate or with obvious open or reticulate venation, often pruinose and papillose below. Flowers usually yellowish, subglobose, subsessile to long-pedicellate, usually 1- or 2-bracteolate, solitary, fascicled, umbellate, racemose or paniculate, the inflorescence often pedunculate, bracteate; sepals in 2-3 whorls of 3, the outer usually shorter and narrower, the inner usually obtuse, oblong to orbicular, as long as or longer than the petals, eglandular; petals usually in 2 whorls of 3, emarginate or rounded, often unguiculate, usually with a basal pair of glands; stamens hypogynous, antepetalous, the anthers bilocular, valvate, the filaments occasionally subapically dentate, apically truncate or apiculate; ovary 1- to 15-ovulate, the stigma capitate, sessile or provided with a prominent style. Berries ellipsoid to globose, red, purple or black, often pruinose, juicy or rather dry, 1- to few-seeded, the seeds yellowish or cyanic.

For a taxonomic revision of the genera *Berberis* and *Mahonia,* both well endowed with American and Asian species, the reader is referred to the work of Ahrendt (in Jour. Linn. Soc. 57: 1. 1961) in which nearly 500 species of *Berberis*

Figure 147. *Berberis nigricans*

and about 100 species of *Mahonia* are recognized, although no Panama specimens of either genus are cited. Only one species of the often-cultivated genus *Berberis*, has been recorded from Panama.

1. Berberis nigricans O. Ktze. Rev. Gen. 1: 10. 1891.

Profusely branching armed shrubs to as much as 4 m. tall, the rather smooth branches glabrous, armed with 3-pronged barbs as much as 2 cm. long. Leaves crowded on spur branches in the axils of the barbs, the blades coriaceous, evergreen, narrowly to broadly obovate, apically obtuse and apiculate, scantily spinulose, basally cuneate, subsessile, 1.5-7.0 cm. long, 0.8-2.4 mm. broad, lustrous above, pruinose, papillose and often resin-dotted below, the venation reticulate, the alate petioles 0.5-4.5 mm. long. Flowers subglobose, orangish, in bracteate simple or scantily branched racemes terminating the spur shoots; bracts lanceolate, caudate, 2-5 mm. long, the pedicels 3-15 mm. long, usually terminated by 1-2(-3) bracteoles (prophylls) subtending the calyx, the bracteoles deltoid to oblong, acute to acuminate, shorter than the sepals; sepals in 2-3 whorls of 3, the outermost deltoid, acute, 1-2 mm. long, the median and innermost broadly obovate to orbicular, obtuse or rounded, 3-5 mm. long, 2-4 mm. broad, glabrous, obscurely nerved; petals 6, broadly obovate, unguiculate, obtuse, or somewhat emarginate, often cucullate and laterally involute, 3-5 mm. long; stamens 6, 3-4 mm. long, the connectives truncate, the anthers bilocular, valvate; ovary ellipsoid, 2- to 4-ovulate, the stigma capitate, subsessile, the style to 1 mm. long (in Panama). Fruit baccate, blackish with a pruinose bloom, ellipsoid, 6-10 mm. long, the style and stigma to 1.5 mm. long.

Costa Rica and Panama at rather high elevations.

Chiriquí: around El Potrero Camp, Chiriquí Volcano, alt. 2800-3000 m., *Pittier 3074;* Potrero Muleto, Volcán Chiriquí, Boquete District, 10,400 ft., *Davidson 1033.*

It is not apparent from Ahrendt's revision whether or not he saw the type of *B. nigricans*, but I would assume from the terse nature of his description that he had not. No mention is made in his account, or in the original description, of the stout three-pronged barbs which characterize the specimens cited above. In spite of this, the short style, and the tendency of the panicle to have few branches, I feel rather certain of the identity of the Panama specimens, with little more than the geography taken into consideration. No other species are reported from Central America. *B. dealbata* Lindl., described from questionably Mexican material, representing the northernmost extension of the *Australes* group. Judging from Ahrendt's geographical resumé of the section *Truxillenses*, another species occurs in Nicaragua.

MENISPERMACEAE

By D. G. RHODES

Woody or subherbaceous twining or scrambling shrubs, rarely small trees. Leaves alternate, simple, entire to crenate, pinnately or palmately nerved, petiolate, exstipulate. Flowers dichlamydeous, dioecious. Staminate inflorescence axillary, frequently fasciculate, basically cymose, frequently racemiform or paniculiform, rarely spiciform. Staminate flowers actinomorphic: Sepals 2- to 3-merous, usually 6, free or rarely united at the base, imbricate or valvate, the interior cycle usually conspicuously larger than the exterior; petals 2- to 3-merous, usually 6, frequently minute, free or rarely united, imbricate or valvate; stamens opposite and equaling the petals in number, the filaments free or variously coherent, the anthers often immersed within the connective, dehiscing longitudinally. Pistillate inflorescence axillary, frequently fasciculate, cymose or racemose, Pistillate flowers actinomorphic, rarely zygomorphic: Sepals 3-merous, usually 6, rarely reduced to 1; petals usually 6, rarely reduced to 1, usually minute; staminodia frequently 6 or absent; carpels 3 or 6, rarely 1, free or connivent; style often recurved or inconspicuous; stigma lingulate, radiate-incised or 3-lobed; ovule 1, amphitropous. Drupes free, sessile or stipitate, erect or hippocrepiform; exocarp membranous or subcoriaceous; mesocarp more or less pulpy; endocarp chartaceous or osseous, often verrucose and ribbed, rarely smooth; embryo usually curved, rarely erect; albumen copious, scanty or absent, frequently ruminate.

A family of about 70 genera and 400 species. North and South America, Africa, northern Australia, Indo-Malayan region, eastern Asia and the Mediterranean basin.

a. Staminate flower with 6-18 sepals, the petals free, the stamens 6, the filaments more or less connate or free; pistillate flower with sepals and petals similar to the staminate.

  b. Old stems conspicuously lenticellate; leaves as broad as long or nearly so, membranous or subcoriaceous; sepals 6-18.

    c. Staminate inflorescence paniculiform; leaves rarely under 12 cm. long, white and woolly below; carpels 6; drupes 6 (or few aborted), exocarp scarcely fleshy, endocarp chartaceous-coriaceous, essentially smooth, exalbuminous ..... 1. CHONDRODENDRON

    cc. Staminate inflorescence racemiform, rarely paniculiform; leaves rarely over 12 cm. long, pubescent or glabrous below; carpels 3; drupes 1-3, exocarp fleshy, endocarp verrucose-ribbed, albuminous. ..... 2. ODONTOCARYA

  bb. Old stems not conspicuously lenticellate; leaves longer than broad, coriaceous; sepals 6.

    d. Petals so greatly involute as to almost conceal the stamens fixed on the claw; leaves rarely exceeding 10 cm. in length; drupe rarely less than 16 mm. in length, albuminous ..... 3. ANOMOSPERMUM

    dd. Petals moderately involute, not concealing the stamens; leaves rarely less than 10 cm. in length; drupe rarely exceeding 16 mm. in length, exalbuminous ..... 4. HYPERBAENA

aa. Staminate flower with 4 sepals, the petals connate, the stamens 4, the filaments coherent forming a staminal column; pistillate flower with 1 sepal and 1 petal ..... 5. CISSAMPELOS

1. CHONDRODENDRON Ruiz & Pav.

Chondrodendron Ruiz & Pav. Prodr. Fl. Peruv. 132. 1794 (as *Chondodendron*); Miers, in Ann. Nat. Hist. ser. 3. 19: 187. 1867.

Botryopsis Miers, loc. cit. ser. 2. 7:43. 1851.
Detandra Miers, loc. cit. ser. 3. 13:124. 1864.

Twining shrubs. Leaves alternate, petiolate. Staminate inflorescence axillary, fasciculate, paniculiform. Staminate flowers 3-merous, actinomorphic: Sepals 6-22, the exterior minutely bracteoliform, the interior 6 conspicuously larger, usually reflexed or sometimes cucullate at the apex in anthesis; petals 6, minute, antesepalous, appressed to the androecium; stamens 6, antepetalous, greatly surpassing the petals, inflexed, the filaments free or slightly coherent at the base, the longitudinally dehiscing anthers 2-celled, the cells separated by and sometimes immersed within a fleshy connective which is often produced beyond the thecae. Pistillate inflorescence axillary, solitary or fasciculate, racemose. Pistillate flowers: Sepals and petals similar to the staminate; staminodia minute or none; carpels 6, erect, gibbose-ellipsoid, the style almost wanting, the stigma lingulate and reflexed. Drupes 6 or a few aborted, gibbose-ellipsoid; endocarp chartaceous-coriaceous, divided by a septum which extends from the base beyond the center; seed deeply hippocrepiform, exalbuminous.

About 10 species. Panama, South America.

Throughout the literature involving the Menispermaceae Ruiz and Pavón's original spelling *Chondodendron* has been adopted by some authors, including Diels, while others have utilized the form *Chondrodendron*. As pointed out by Sandwith (in Kew Bull. 58. 1955), Ruiz and Pavón stated that they called their new genus *Chondodendron* because of the "abundance of burrs" on the trunk and branches of the "tree," referring to the verrucose-lenticellate cortex of the woody stems. The name therefore clearly must have been derived from the Greek χόνδρος, "burr" and δένδρον, "tree" and the name should be spelled *Chondrodendron*. Sandwith proposes that the original spelling *Chondodendron* be treated as an orthographic error, and that the correct spelling *Chondrodendron* be adopted in the future for this genus. On the basis of the evidence, the spelling *Chondrodendron* is adopted for use in this paper.

1. Chondrodendron tomentosum Ruiz & Pav. Syst. Veg. 261. 1798.

Epibaterium ? tomentosum Pers. Syn. Pl. 2:561. 1807.
Cocculus chondodendron DC. Syst. 1:552. 1818.
Chondodendron scabrum Miers, in Ann. Nat. Hist. ser. 2. 7:44. 1851.
Botryopsis spruceana Eichl. in Flora 47:394. 1864.
Chondodendron cretosum Miers, in Ann. Nat. Hist. ser. 3. 19:192. 1867, nom. nud.; Contrib. Bot. 3:312. 1871.
Chondodendron hypoleucum Standl. in Contrib. Arn. Arb. 5:65, *pl, 10,* 1933.

Shrubby twiners; stems striate with the bark of older stems verrucose-lenticellate, minutely puberulent to tomentose, rarely glabrous. Leaves petiolate, ovate, deltoid or suborbicular, entire to crenate, the apex obtuse or acute, mucronate or sometimes emarginate, the base cordate, subcordate or truncate, 10-18 cm. long,

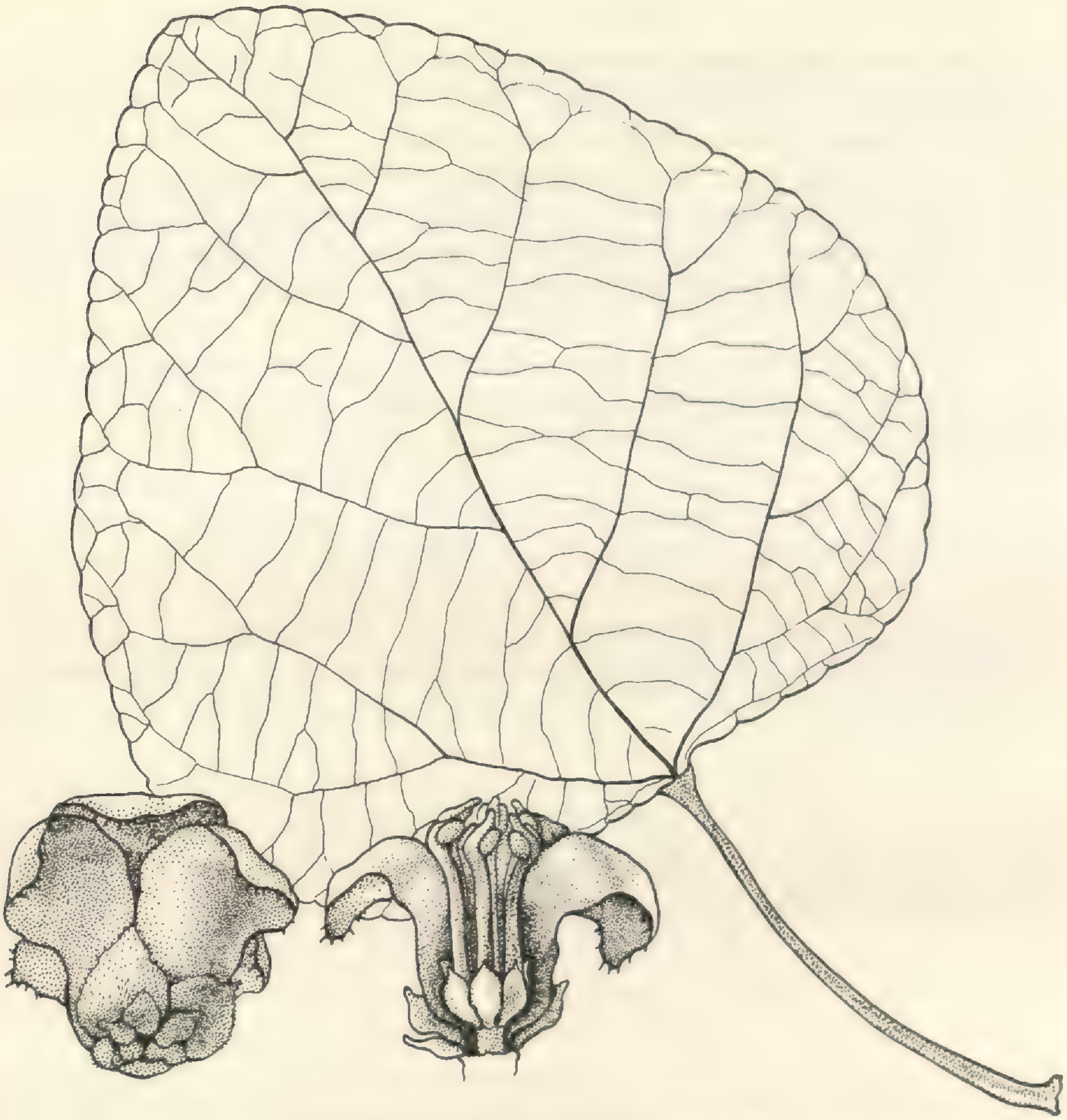

Figure 148. *Chondrodendron tomentosum*

9-18 cm. wide, at length subcoriaceous, 5-, 7- or 9-pli-nerved, glabrous above, white and woolly beneath; petioles distally and proximally swollen, 4-14 cm. long, puberulent to tomentose. Staminate inflorescence fasciculate in the leaf axils, paniculiform, 6 cm. or more in length, the rachis tomentose; bracts and bracteoles ovate, about 0.5 mm. long. Staminate flowers (in Panama): Sepals 9, 14, or 16, irregularly imbricate, the 3, 8, or 10 exterior small, broadly ovate, rounded or obtuse at the apex, 0.5-1.4 mm. long, 0.5-1.2 mm. wide, exteriorly tomentose or with the margins ciliolate, the 6 interior conspicuously larger, oblong-ovate, 2.5-3.0 mm. long, 1.5-1.7 mm. wide, glabrous or with the margins ciliolate; petals 6, minute, broadly ovate or lanceolate, acute or acuminate at the apex, 0.5-0.8 mm. long, 0.3-0.5 mm. wide, glabrous; stamens 6, 1.5 mm. long, inflexed, the connective produced beyond the thecae, the filaments free or coherent at the base. Pistillate flower or fruit not seen.

Peru, Bolivia, Colombia and Panama.

CANAL ZONE: Barro Colorado Island, shore east of Gross Trail, *Woodworth & Vestal* 438, Gatún Lake, altitude 120 meters or less, *Standley 40849, 41007, 41155.*

Three distinct types of staminate flowers are recognized by Krukoff and Moldenke (in Brittonia 3: 17. 1938) in *Chondrodendron tomentosum*. Type I is described as having 15 sepals with the outer 9 being 0.7-1.6 mm. long and 0.7-1.3 mm. wide, acute at the apex, fleshy, and slightly connate at the base. The 6 inner sepals are 3-4 mm. long, 1.7-2.5 mm. wide, campanulate-tubular at the base and glabrate except for the more or less fringed-ciliolate margins. The 6 petals are well-developed, broadly elliptic or obovate, about 0.5 mm. long and 0.25 mm. wide and rounded at the apex. The 6 stamens are about 2 mm. long. This is the *Botryopsis spruceana* type of staminate flower. Type II has (15-)19-22 sepals about 0.7 mm. long and 0.5 mm. wide which are glabrous throughout. The 6 petals are very minute, about 0.2 mm. long and wide, broadly elliptic and obtuse or rounded at the apex. The 6 stamens are about 1.2 mm. long with the anthers about as long as the filaments. This type represents the true *Chondrodendron tomentosum* type of staminate flower. Type III is described above and is based upon the *Chondrodendron hypoleucum* of Standley. Representatives of the three groups cannot be distinguished vegetatively.

2. ODONTOCARYA Miers.

ODONTOCARYA Miers, in Ann. Nat. Hist. ser. 2. 7: 38. 1851.

Chondodendron acc. to Benth. & Hook. f. Gen. 1:34. 1862, not Ruiz & Pav.

Twining or scrambling shrubs. Leaves alternate, petiolate. Staminate inflorescence axillary, solitary, racemiform, rarely paniculiform. Staminate flowers 3-merous, actinomorphic: Sepals 6-18, the exterior bracteoliform, the interior conspicuously larger, imbricate; petals 6, carnose, antesepalous; stamens 6, antepetalous, the filaments more or less coherent, dehiscence longitudinal. Pistillate inflorescence axillary, solitary, racemose. Pistillate flowers: Sepals and petals similar to the staminate; staminodia 6 or wanting; carpels 1-3, gibbose-oblong, the stigma sessile, 3-lobed. Fruit an ovoid-ellipsoidal drupe.

About 10 species. Lesser Antilles, Central America and South America.

a. Leaves lustrous; staminate inflorescences borne on short congested secondary branches; sepals 18; petals 0.6-0.7 mm. long, pubescent ..... 1. O. NITIDA

aa. Leaves dull; staminate inflorescences arising directly from main stem; sepals 6; petals 0.7 mm. or more in length, glabrous.

b. Leaves with glandular areas between the base of the midrib and lowest diverging nerves, the base usually cordate; staminate inflorescence racemiform; petals 1.5-2.6 mm. long ..... 2. O. PAUPERA

bb. Leaves not glandular, the base usually truncate; staminate inflorescence paniculiform; petals 0.7-1.2 mm. long ..... 3. O. TRUNCATA

1. ODONTOCARYA NITIDA Riley, in Kew Bull. 119. 1927.

Scrambling shrubs; stems striate, puberulent. Leaves petiolate, the lamina broadly ovate, entire, the apex obtusely caudate-acuminate, the base cordate, 5-11 cm. long, 3-6 cm. wide, subcoriaceous, glabrous above, dark and lustrous, palmately 5- to 7-nerved, puberulent below; petioles 2-4 cm. long, pubescent. Staminate inflorescence a racemiform thyrse, axillary, borne on a short congested leafy secondary branch, 3-6 cm. long, the rachis pubescent; bracts linear, about 1 mm. long. densely pubescent; bracteoles linear, 0.5 mm. long, densely pubescent. Staminate flowers: Sepals 18, ovate to elliptic, 0.8-2.1 mm. long, 0.5-1.2 mm. wide, carnose, the exterior densely pubescent; petals 6, obovate, the apex truncate or rounded, 0.6-0.7 mm. long, 0.3-0.5 mm. wide, carnose, the exterior densely pubescent; stamens 6, 0.7-0.8 mm. long, glabrous, the filaments coherent at the base. Pistillate flower and fruit not seen.

Endemic to Panama.

CANAL ZONE: Cocoli, *Riley 136.*

Riley recognizes no calyx or corolla and refers to the perianth as being comprised of tepals. The six innermost perianth segments, however, are conspicuously small and interrupt a transitional increase in size from the outermost whorl of segments inward. An anatomical distinction exists in that the six innermost segments are provided with a single median nerve characteristic of petals while the outer segments are provided with a single median plus a pair of lateral nerves characteristic of sepals. Bearing in mind the anatomical evidence present and the fact that the family is characterized by the presence of comparatively small petals, I consider the perianth to be dichlamydeous.

2. ODONTOCARYA PAUPERA (Griseb.) Diels, in Engl. Pflanzenr. 4.94: 172. 1910.

Chondodendron hederaefolium Miers, in Ann. Nat. Hist. ser. 2. 7:38. 1851, nom. nud.
Cocculus pauper Griseb. in Gotting. Abh. 7:162. 1857.
Chondodendron tomentosum Benth. in Journ. Linn. Soc. 5: suppl. 2. 47. 1861.
Odontocarya hederaefolia Miers, in Contrib. Bot. 3. 64. 1871.
Odontocarya scabra Miers, loc. cit. 65. 1871.

Climbing or scrambling shrubs; older stems thick and fleshy, conspicuously lenticellate, the younger stems striate, glabrous or essentially so. Leaves petiolate, the lamina broadly ovate to subhastate, entire, the apex acute or obtuse, mucronate, the base cordate or rarely obscurely truncate, 4.5-9.5 cm. long, 3.0-6.0 cm. wide, membranous, pubescent or puberulent above with conspicuous glandular areas between the base of the midrib and lowest diverging nerves, pubescent below; petiole 2.0-8.0 cm. long, pubescent or puberulent. Staminate inflorescence axillary, racemiform, about 7 cm. long, the rachis puberulent; bracts and bracteoles about 1.0-1.5 mm. long. Staminate flowers: Sepals 6, the 3 exterior ovate or elliptic, sparsely toothed, 1.2-2.0 mm. long, 0.6-1.0 mm. wide, membranous, essentially glabrous, the 3 interior conspicuously larger, obovate, the apex obtuse or rounded, 1.8-3.5 mm. long, 1.5-2.2 mm. wide, glabrous; petals 6, elliptic, carnose, 1.5-2.6 mm.

Figure 149. *Odontocarya paupera*

long, 1.0-1.8 mm. wide, glabrous; stamens 6, 1.0-1.8 mm. long, the filaments more or less coherent. Pistillate inflorescence an axillary raceme, about 9 cm. long, the rachis puberulent; bracts and bracteoles about 1.0 mm. long. Pistillate flowers: Sepals and petals similar to the staminate; carpels 1-3, gibbose, free, sessile, the style not evident, the stigma 3-lobed. Drupe ovoid, about 1 cm. long, 0.5 cm. wide; endocarp semi-ellipsoid, verrucose, ribbed.

Panama, Lesser Antilles and northern South America.

CANAL ZONE: Balboa, moist thicket, *Standley 27130;* in Powell Garden, *Standley 41189;* vicinity of Miraflores, *G. White 121;* locality omitted, *Johansen 70.* PANAMÁ: Isla Taboga, ca. 0-186 m., *Woodson, Allen & Seibert 1486;* Las Sabanas, wet thicket, *Standley 40778, Paul 599;* San José Island, Perlas Archipelago, *Erlanson 581, 546, Johnston 7, 786.*

There has been considerable taxonomic confusion and misdetermination between this species and *Odontocarya nitida.* The two species are readily distinguished, however, as *Odontocarya paupera* possesses distinctive glandular areas on the leaf, an essentially glabrous flower with six sepals, and staminate inflorescences which are borne upon the main stem of the vine. *Odontocarya nitida* has a leaf devoid of glandular areas, a pubescent flower with 18 sepals, and staminate inflorescences which are borne on short congested secondary branches.

3. ODONTOCARYA TRUNCATA Standl. in Journ. Arn. Arb. 11: 121. 1930.

Twining shrubs; stems striate, conspicuously verrucose-lenticellate, glabrous. Leaves petiolate, the lamina ovate, the apex acuminate, the base truncate or obscurely cordate, 7-12 cm. long, 5-9 cm. wide, at length subcoriaceous, glabrous, somewhat bullate above; petioles 3-4 cm. long, glabrous. Staminate inflorescence axillary, paniculiform, 8-24 cm. long, the rachis glabrous; bracts 1.0-1.5 mm. long, 0.5 mm. wide; bracteoles scarious, ovate to lanceolate, 0.5-1.0 mm. long. Staminate flowers: Sepals 6, glabrous, the 3 exterior obscurely coherent at the base, ovate to lanceolate, membranous, 0.5-0.8 mm. long, 0.3-0.6 mm. wide, the 3 interior conspicuously larger, ovate to elliptic, the apex obtuse or rounded, the base truncate or rounded, 1.3-1.7 mm. long, 1.0-1.4 mm. wide; petals 6, cuneate, carnose, 0.7-1.2 mm. long, 0.5-0.8 mm. wide, glabrous; stamens 6, about 1 mm. long, the filaments coherent at the base. Pistillate flower not seen. Drupe ovoid, yellow about 1.5 cm. long, 1.0 cm. wide.

Endemic to Panama.

CANAL ZONE: Barro Colorado Island, *Bangham 541, Salvoza 960;* Las Cascadas Plantation, near Summit, *Standley 29519;* Margarita Swamp, south of France Field, *Maxon & Valentine 7046.*

3. ANOMOSPERMUM Miers.

ANOMOSPERMUM Miers, in Ann. Nat. Hist. ser. 2. 7: 39. 1851.

Woody climbers. Leaves alternate, petiolate. Staminate inflorescence axillary, solitary or fasciculate, racemiform or paniculiform. Staminate flowers 3-merous, actinomorphic: Sepals 6, the exterior bracteoliform, the interior conspicuously larger, imbricate; petals 6, so greatly involute as to almost conceal the stamens

by forming a "pseudodisc"; stamens 6, free, dehiscence longitudinal. Pistillate inflorescence axillary, racemose or sessile and umbelliform. Pistillate flowers: Sepals and petals similar to the staminate; staminodia 6; carpels 3, free; stigma subsessile or sessile, lingulate. Drupes 1-3, excentrically stipitate, erect or curved; albumen copious, ruminate.

About 11 species. South America and Panama.

The only representative of this genus thus far collected in Panama (COCLÉ, El Valle de Antón, *Allen* 3538) is perhaps a new species but the absence of flowering material prevents an adequate analysis at this time. This specimen is closely related to *Anomospermum reticulatum* (Mart.) Eichl. of the Amazon basin in that the extremely dense venation reticulum of the lamina is as conspicuous beneath as above, but differs in the glabrous petioles and the absence of any pubescence on the lower leaf surface.

4. HYPERBAENA Miers.

HYPERBAENA Miers, in Ann. Nat. Hist. ser. 2. 7: 44. 1851.

Pachygone Eichl. in Denkschrift. Bot. Gesellsch. Regensb. 5:1. 1864.

Woody twiners or sometimes erect shrubs or small trees. Leaves alternate, petiolate. Staminate inflorescence axillary, fasciculate, spiciform or racemiform. Staminate flowers 3-merous, actinomorphic: Sepals 6, the exterior bracteoliform, the interior conspicuously larger, imbricate; petals 6, antesepalous; stamens 6, antepetalous, free or the filaments connate at the base, dehiscence longitudinal. Pistillate inflorescence axillary, solitary, racemose. Pistillate flowers: Sepals and petals similar to the staminate; staminodia 6; carpels 3, free, gibbose; style reflexed. Drupes sessile, curved; exalbuminous.

About 40 species. Mexico, Central America, South America and the Antilles.

a. Woody twiners; leaves palmately 5-nerved; inner sepals 2.5-4.0 mm. long, densely pubescent; petals pubescent; stamens cucullate, pubescent .....1. H. PANAMENSIS

aa. Small trees; leaves pinnately nerved; inner sepals 1.1-1.4 mm. long, glabrous or essentially so; petals glabrous; stamens erect, glabrous .....2. H. ALLENII

1. HYPERBAENA PANAMENSIS Standl. in Journ. Wash. Acad. Sci. 15: 474. 1925.

Hyperbaena hondurensis Standl. in Field Mus. Pub. Bot. 4:305. 1929.

Woody vines; stem striate with the bark of older stems conspicuously lenticellate, puberulent or glabrous. Leaves petiolate, elliptic, ovate or oblong, entire, the apex abruptly acute, acuminate or obtuse, mucronate, the base obtuse, rounded or truncate, 6-24 cm. long, 3-14 cm. wide, at length coriaceous, palmately 5-nerved, frequently with a pinnate aspect, the basal nerves frequently slender and inconspicuous, glabrous above, sparsely and minutely puberulent or glabrous below; petioles swollen distally, 1-9 cm. long, glabrous to puberulent. Staminate inflorescence fasciculate or solitary in the leaf axils, racemiform, up to 20 cm. in length, the rachis pubescent to tomentose; bracts and bracteoles ovate to linear, about 1 mm. long, densely pubescent. Staminate flowers: Sepals 6, the 3 outermost small, ovate, 0.7-1.2 mm. long, 0.5-0.8 mm. wide, exteriorly pubescent, the 3

innermost conspicuously larger, broadly ovate, 2.5-4.0 mm. long, 2.2-2.5 mm. wide, exteriorly pubescent; petals 6, minute, spatulate to oblong, about 0.5 mm. long, exteriorly pubescent; stamens 6, cucullate, about 1.3 mm. long, densely pubescent, the anthers immersed within the connective, the filaments free or rarely coherent at the base. Pistillate inflorescence solitary or fasciculate in the leaf axils, racemose, about 8 cm. long, the rachis tomentose; bracts and bracteoles ovate to linear, about 0.5-1.0 mm. long, densely pubescent. Pistillate flowers: Sepals and petals similar to the staminate; staminodia 6, about 2.5 mm. long, pubescent at the base; carpels 3, gibbose, sessile, the style not evident, the stigma radiate-incised. Drupe obovoid, 1.5-2.5 cm. long, puberulent or glabrous.

Panama, Costa Rica, Guatemala, Honduras and British Honduras.

CANAL ZONE: Barro Colorado Island, *Bangham 484, Bailey 101, Standley 40978, 40800, 40787, 41077, Wetmore & Woodworth 76;* Gamboa, *Standley 28417.*

Considerable deliberation involved the placing of *Hyperbaena hondurensis* into synonomy. In 1925 Standley described *Hyperbaena panamensis* (*Standley 28417*) from sterile material. The distinguishing characteristic was the venation. A palmately 5-nerved condition provided a pair of slender and inconspicuous basal nerves, a prominent midrib, and a prominent pair of inner nerves extending almost to the apex of the leaf so as to impart a subparallel effect.

In 1929 Standley described *Hyperbaena hondurensis* (*Standley 55220*), once again from sterile material. A palmately 5-nerved condition existed here also but the inner pair of nerves extended approximately half the length of the leaf and several lateral nerves originated from the midrib. This afforded a pinnate aspect to the leaf.

Specimens from Panama and Costa Rica illustrate the *Hyperbaena panamensis* type of venation while those of Honduras, Guatemala and British Honduras the *H. hondurensis* type. Unfortunately, no specimens from Nicaragua are available. The *Hyperbaena panamensis* type of leaf is provided with somewhat more pubescence on the lower surface and has a somewhat shorter petiole than the *Hyperbaena hondurensis* type.

Vegetatively, it appears that two species exist. However, floral examination involving the two types indicates the opposite view as no floral distinction can be formulated between the two. Furthermore, the pubescent petals, cucullate stamens, and connivent carpels present very distinctive floral characteristics thereby making their appearance in separate species quite unlikely. Along this line of thought is the marked contrast between the floral characteristics noted above and allied species of the genus, for example, *Hyperbaena allenii.*

In summary it can be stated that although considerable variation exists vegetatively, the floral similarity between *Hyperbaena panamensis* and *H. hondurensis* unite them as one species—*H. panamensis* by precedence.

2. HYPERBAENA ALLENII Standl. in Ann. Missouri Bot. Gard. 27:310. 1940.

Small trees; young stems striate, densely pubescent. Leaves petiolate, lanceolate-oblong, entire, the apex acute or obtuse, the base obtuse or rounded, 14-23 cm.

Figure 150. *Hyperbaena allenii*

long, 4.5-6.0 cm. wide, subcoriaceous, pinnately nerved, glabrous above, puberulent below; petioles swollen distally, 1.5-3.0 cm. long, densely pubescent. Staminate inflorescence axillary, fasciculate, spiciform, 0.5-3.0 cm. long, the rachis densely pubescent; bracts and bracteoles about 0.5 mm. long, densely pubescent. Staminate flowers; Sepals 6, the 3 outermost small, obovate, obscurely toothed, 0.7-0.9 mm. long, 0.5-0.6 mm. wide, exteriorly pubescent, the 3 innermost conspicuously larger, obovate, obscurely toothed, 1.1-1.4 mm. long, 0.7-0.9 mm. wide, glabrous or with the margins ciliolate; petals 6, obovate, 0.5-0.8 mm. long, 0.3-0.5 mm. wide, glabrous; stamens 6, free, about 1 mm. long, glabrous. Pistillate flower not seen. Fruit ovoid, about 2 cm. long, glabrous.

Endemic to Panama.

COCLÉ: north rim of El Valle de Antón, 600-1000 m., *Allen 1656;* north of El Valle de Antón, trail to Las Minas, alt. about 1000 m., *Allen 2465;* Loma del Tigre, region north of El Valle de Antón, alt. 1000 m., *Allen 3807.*

5. CISSAMPELOS L.

CISSAMPELOS L. Sp. Pl. 1031. 1753.

Dissopetalum Miers, in Ann. Nat. Hist. ser. 3. 17:267. 1866.

Twining shrubs, rarely erect. Leaves alternate, petiolate, more or less peltate or basifixed. Staminate inflorescence axillary, generally fasciculate, normally originating in a leafy axil as multiflowered dichasia or the dichasia originating on axillary secondary branches in the axils of reduced leaves or bracts. Staminate flowers 2-merous, actinomorphic: Sepals 4, usually exteriorly pubescent; petals connately cupulate; stamens 4, the anthers sessile on a column formed by the connate filaments, dehiscence transverse. Pistillate flowers fasciculate in the axils of reduced leaves or bracts upon secondary, frequently fasciculate, axillary branches, zygomorphic: Sepal 1, obovate, exteriorly pubescent; petal 1, antesepalous; carpel 1, free, gibbose, the style short, the stigma 3-lobed. Drupes subglobose; endocarp osseous, verrucose, ribbed.

A troublesome genus of about 25 species. North and South America, Africa, Asia and Australia.

a. Leaves conspicuously peltate, the base usually truncate or rounded, indument when present sericeous with long whitish hairs; bracts of secondary axillary branches large and foliaceous; carpels essentially glabrous; drupes 5-7 mm. long ..... 1. C. TROPAEOLIFOLIA

aa. Leaves generally obscurely peltate or basifixed, the base cordate, rarely truncate or rounded, indument sericeous or tomentose with short reddish-yellow, yellowish-brown or whitish hairs; bracts of secondary axillary branches usually much reduced; carpels densely pubescent; drupes 2.5 mm. long.

b. Leaves puberulent above, pubescent below; staminate inflorescence commonly arising from the axils of bracts upon secondary, generally fasciculate, axillary branches; sepals of staminate and pistillate flowers with conspicuous red spotting; drupes 2-4 mm. long. ..... 2. C. FASCICULATA

bb. Leaves usually more or less pubescent above and below; staminate inflorescence commonly arising from normal leaves; sepals of staminate and pistillate flowers without conspicuous red spotting; drupes 4-5 mm. long. ..... 3. C. PAREIRA

The frequent appearance of *Cissampelos grandifolia* Triana & Planch. in Costa Rican and Colombian collections suggests its probable presence in Panama. Although several specimens have been misdetermined as *Cissampelos grandifolia*, I do not find the species to have been collected in Panama. The species is distinguished by its much-branched and spreading paniculiform inflorescence and the large, conspicuously peltate, broadly ovate to suborbicular, long-petiolate leaves.

1. Cissampelos tropaeolifolia DC. Syst. 1:532. 1818.

Cissampelos membranacea Triana & Planch. in Ann. Sc. Nat. ser. 4. 17:43. 1862.

Subherbaceous twiners; stems striate, pubescent or puberulent, rarely glabrous. Leaves petiolate, conspicuously peltate, ovate to suborbicular, entire to crenate, the apex obtuse, rounded or acuminate, mucronate, the base truncate or rounded, rarely cordate, 5-11 cm. long, 5-10 cm. wide, membranous, palmately nerved, sericeous with long whitish hairs or glabrous above, paler and occasionally glaucous below, sericeous or puberulent; petioles 4-9 cm. long, tomentose to glabrous. Staminate inflorescence multiflowered fasciculate dichasia in the leaf axils or upon short secondary axillary branches within the axils of reduced leaves or bracts, the two forms frequently occurring together; bracts of secondary branches large and foliaceous, basifixed, sessile or obscurely petiolate, broadly cordate to subreniform, mucronate, 5-15 mm. long, 4-25 mm. wide, membranous, puberulent to densely pubescent; bracteoles linear, about 0.5 mm. long, pubescent. Staminate flowers: Sepals 4, ovate, oblong or obovate, 1.0-1.4 mm. long, 0.8-1.0 mm. wide, glabrous or exteriorly puberulent; corolla campanulate, 0.5-1.0 mm. in diameter, glabrous; anthers 4, glabrous. Pistillate inflorescence composed of individual flowers fasciculate in the axils of bracts upon secondary axillary branches. Bracts and bracteoles similar to the staminate. Pistillate flowers: Sepal 1, ovate to obovate, 1.0-1.2 mm. long, 0.8-1.0 mm. wide, glabrous or puberulent; petal 1, suborbicular, 0.5-0.7 mm. long, 0.5-1.0 mm. wide; carpel 1, gibbose, sessile, essentially glabrous, the stigma 3-lobed. Drupe red, obovoid, compressed, 5-7 mm. long, 4-5 mm. wide, pubescent, rarely glabrous; endocarp ribbed, verrucose.

Southern Mexico, Central America and northern South America.

Bocas del Toro: Chiriquí Lagoon, *Von Wedel 1853, 1119, 1376, 1372, 1035;* Isla Colón *Von Wedel 46, 2947;* Old Bank Island, *Von Wedel 2083, 1888, 1991, 1985;* Water Valley *Von Wedel 673, 1819, 1490;* Chiriquí Lagoon region, Punta Rovalo and Rovalo River, *Seibert 1563;* Columbus Island, *Von Wedel 23;* no locality given but presumably Chiriquí Lagoon or vicinity, *Von Wedel 381*, 382, 382. Canal Zone: Barro Colorado Island, *Standley 41002, Shattuck 430;* near mouth of R. Chagres, *Allen 897;* Gatún, *Stevens 1342;* Mount Hope Cemetery, *Standley 28789;* between Mount Hope and Santa Rita Trail, *Cowell 94.* Colón: between France Field and Cativa1, *Standley* 30345. Chiriquí: Río Chiriquí to Remedios, ca. 15-50 m., *Woodson, Allen & Seibert* 1187; between R. Tinta and R. Tabasará, along main highway, *Woodson, Allen & Seibert 414;* vicinity of San Félix, alt. 0 to 120 m., *Pittier* 5458. Darién: Cana and vicinity, 2000-6500 ft. el., *Williams 778;* Paca below Cana, *Williams 767.*

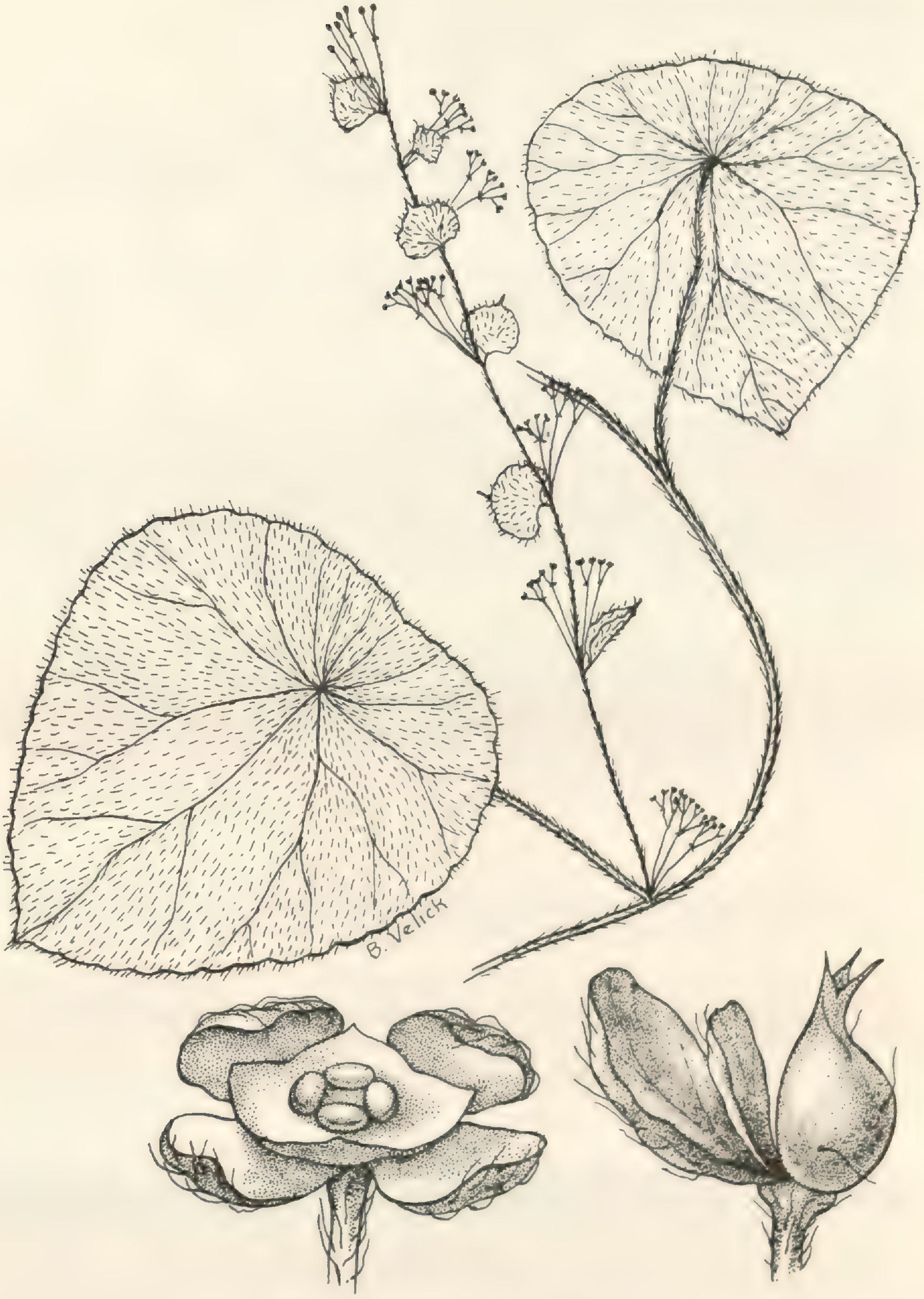

Figure 151. *Cissampelos tropaeolifolia*

2. Cissampelos fasciculata Benth. in Lond. Journ. Bot. 2:361. 1843.

Cissampelos scutigera Triana & Planch. in Ann. Sc. Nat. ser. 4. 17:42. 1862.
Cissampelos myriocarpa Triana & Planch., loc. cit. 1862.
Cissampelos andromorpha Eichl. in Mart. Fl. Bras. 13. 1:195. 1864.
Cissampelos floribunda Miers, in Ann. Nat. Hist. ser. 3. 17:135. 1866.
Cissampelos coriacea Standl. in Field Mus. Pub. Bot. 18:437. 1937.

Shrubby twiners; stems striate, puberulent to tomentose. Leaves petiolate, conspicuously or obscurely peltate or basifixed, broadly ovate to suborbicular, entire, the apex obtuse, rounded or acute, mucronate, the base cordate or truncate, rarely rounded, 4-14 cm. long, 5-15 cm. wide, membranous to subcoriaceous, palmately 5- to 9-nerved, puberulent and dark above, paler below and sericeous or tomentose with reddish-yellow, yellowish-brown or whitish hairs; petioles twisted and swollen proximally, 4-11 cm. long, pubescent or more commonly tomentose. Staminate inflorescence multiflowered fasciculate dichasia originating upon secondary axillary branches within the axils of reduced leaves or bracts, rarely axillary from normal leaves; peduncle of cymes at length 1.5 cm. long, densely pubescent; bracts of secondary branches basifixed, sessile or petiolate, ovate to subreniform, mucronate, generally conspicuously involute, pubescent; bracteoles about 1 mm. long, pubescent. Staminate flowers: Sepals 4, obovate, 0.8-1.5 mm. long, 0.5-0.8 mm. wide, exteriorly pubescent, the interior with conspicuous red spotting; corolla cupulate, 0.6-1.0 mm. in diameter, sparsely pubescent or glabrous; anthers 4, glabrous. Pistillate inflorescence composed of individual flowers fasciculate in the axils of bracts upon fasciculate secondary, frequently branched, axillary branches; bracts and bracteoles similar to the staminate. Pistillate flowers: Sepal 1, obovate, 1.0-2.0 mm. long, exteriorly pubescent, the interior with conspicuous red spotting; petal 1, suborbicular, 0.5-0.8 mm. long, 0.7-1.0 mm. wide; carpel 1, gibbose, pubescent. Drupe obovoid, compressed, 2-4 mm. long and wide, pubescent; endocarp ribbed, verrucose.

Nicaragua, Costa Rica, Panama and northern South America.

chiriquí: vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m., *Woodson & Schery* 545; vicinity of Bajo Chorro, alt. 1900 m., *Woodson & Schery* 682.

After extensive examination of available material no significant distinction could be ascertained between *Cissampelos coriacea* Standl. and *C. fasciculata*, therefore the former is placed in synonomy.

Vegetatively this species tends to be quite variable. Specimens from Costa Rica habitually bear large obscurely peltate or basifixed leaves which are broadly cordate. Panamanian and Colombian material, on the other hand, has a tendency toward smaller suborbicular leaves which are conspicuously peltate.

3. Cissampelos pareira L. Spec. Pl. 1031. 1753.

Cissampelos pareira α L., loc. cit. 1753.
Cissampelos caapeba L. loc. cit. 1032. 1753.
Cissampelos cocculus Poir. in Lam. Encycl. 5:9. 1804.
Cissampelos heterophylla DC. Syst. 1:534. 1818.
Cissampelos microcarpa DC. loc. cit. 1818.

Cissampelos discolor DC. loc. cit. 1818.
Cissampelos tomentosa DC. loc. cit. 1818.
Cissampelos tamoides Willd. ex DC. loc. cit. 536. 1818.
Cissampelos argentea H.B.K. Nov. Gen. & Sp. 5:67. 1821.
Cissampelos guayaquilensis H.B.K. loc. cit. 1821.
Cissampelos orinocensis H.B.K. loc. cit. 68. 1821.
Cissampelos monoica St. Hil. Fl. Bras. Mer. 1:55. 1825.
Cissampelos australis St. Hil. loc. cit. 56. 1825.
Cissampelos haenkeana Presl. Rel. Haenk. 2:80. 1836.
Cissampelos hirsutissima Presl. loc. cit. 1836.
Cissampelos kohautiana Presl. loc. cit. 81. 1836.
Cissampelos acuminata Benth. Pl. Hartw. 445. 1839, not DC.
Cissampelos canescens Miq. Sert. Exot. 7. *t. 4* 1842.
Cissampelos glaucescens Triana & Planch. in Ann. Sc. Nat. ser. 4. 17:41. 1862.
Cissampelos subreniformis Triana & Planch. loc. cit. 1862.
Cissampelos longipes Miers, in Ann. Nat. Hist. ser. 3. 17:134. 1866, nom. nud.; Contrib. Bot. 3:139. 1871.
Cissampelos testudinaria Miers, loc. cit. 1866, nom. nud.; loc. cit. 143. 1871.
Cissampelos limbata Miers, loc. cit. 1866, nom. nud.; loc. cit. 1871.
Cissampelos benthamiana Miers, loc. cit. 1866, nom. nud.; loc. cit. 144. 1871.
Cissampelos auriculata Miers, loc. cit. 135. 1866, nom. nud.; loc. cit. 158. 1871.
Cissampelos hederacea Miers, loc. cit. 1866, nom. nud.; loc. cit. 159. 1871.
Cissampelos consociata Miers, loc. cit. 1866, nom. nud.; loc. cit. 167. 1871.
Cissampelos diffusa Miers, loc. cit. 136. 1866, nom. nud.; loc. cit. 168. 1871.
Cissampelos pareira var. δ. *monoica* Eichl. in Mart. Fl. Bras. 131:190. 1894.
Cissampelos pareira f. *reinformis* and f. *emarginato-mucronata* Chod. & Hassl. in Bull. Herb. Boiss. ser. 2. 3:420. 1903.

Shrubby twiners; stems striate, glabrous to tomentose. Leaves petiolate, obscurely peltate or basifixed, broadly ovate, entire, the apex obtuse, rarely acuminate, frequently somewhat emarginate, mucronate, the base truncate or cordate, 2-12 cm. long and wide, membranous or papery, palmately 3- to 7-nerved, in youth more or less sericeous-tomentose on both sides, at length above more or less pubescent, rarely glabrous, below frequently paler, tomentose or pubescent, rarely entirely glabrous. Staminate inflorescence multiflowered fasciculate dichasia in the leaf axils, sometimes upon secondary axillary branches within the axils of reduced leaves or bracts; bracts of secondary branches basifixed, sessile or obscurely petiolate, ovate to subreniform, mucronate, about 1 cm. long and wide to minute, membranous, pubescent to tomentose; bracteoles linear, about 0.5 mm. long, pubescent. Staminate flowers: Sepals 4, ovate to obovate, exteriorly pubescent, 1.0-2.0 mm. long, 0.5-1.2 mm. wide; corolla campanulate, 0.8-1.8 mm. in diameter; anthers 4, glabrous. Pistillate inflorescence composed of individual flowers fasciculate upon secondary axillary branches within the axils of reduced leaves or bracts; bracts basifixed, sessile or obscurely petiolate, broadly ovate to reniform, mucronate, about 1.5 mm. long, 2.0 mm. wide to minute, membranous, puberulent to tomentose. Pistillate flowers: Sepal 1, obovate, 1.0-2.0 mm. long, 0.5-0.8 mm. wide, exteriorly pubescent; petal 1, broadly obovate to reniform, 0.5-0.8 mm. long, 0.7-1.5 mm. wide, glabrous or puberulent; carpel 1, gibbose, densely pubescent. Drupe broadly obovate or suborbicular, compressed, 4-5 mm. long, 3-4 mm. wide, pubescent or puberulent; endocarp verrucose, ribbed.

Southern Mexico, Central America, South America, Antilles, eastern Africa, India, Malaya, Indonesia, Philippines, northern Australia and Madagascar.

BOCAS DEL TORO: Chiriquí Lagoon, *Von Wedel 1309;* Shepherd Island, *Von Wedel 2691.* CANAL ZONE: Barro Colorado Island, *Aviles 921, 57, 888, Shattuck 476, Bailey & Bailey 575, Wetmore & Abbe 177, 178;* Bismark above Penonomé, *Williams 536;* Balboa, *Standley 25526;* Chagres, *Fendler 4;* Chivi-Chivi Trail, 2 miles above Red Tank, *Maxon & Harvey 6578;* Darién Station, *Standley 31642;* Empire to Mandinga, *Piper 5480;* Gatún, *Hayes 1035;* Juan Mina, *Piper 5688;* Las Cascadas Plantation, near Summit, *Standley 25672;* in government forest along Las Cruces Trail, 75 m., *Hunter & Allen 752;* Mamei Hill, alt. 20 to 90 m., *Pittier 3796;* Obispo, *Standley 31773;* Río Grande, near Culebra, alt. 50 to 100 m., *Pittier 2092;* Fort Kobbe road, *Woodson, Allen & Seibert 1425, 1426;* thickets north of Summit, *Woodson, Allen & Seibert 766;* vicinity of Miraflores, *P. White 120, G. White 122;* western slope of Ancón Hill, *Woodson, Allen & Seibert 1324;* around Culebra, alt 50 to 150 m., *Pittier 2218;* Old Experiment Station, 3 miles east of Panama City, *Maxon, Harvey & Valentine 7085.* CHIRIQUÍ: Boquete, *Davidson 611;* Cerro Vaca, eastern Chiriquí, in forest or in thickets, alt. 900 to 1136 m., *Pittier* 5323. COCLÉ: El Valle de Antón, alt. 600 m., *Allen 3705;* mountains beyond La Pintada, 400-600 m., *Hunter & Allen 581.* DARIÉN: locality missing, *Macbride 2699.* PANAMÁ: Bella Vista, *Bro. Heriberto 221;* vicinity of Bella Vista, *Piper 5370;* near Tapía River, Juan Díaz region, *Maxon & Harvey 6760;* Sabanas, *Bro. Paul 21, 40;* Sabanas near Chepo, 30 m., *Hunter & Allen 91.*

Diels divides *Cissampelos pareira* into nine varieties of which only two, var. α. *typica* and var. γ. *haenkeana,* occur in Panama. The former is characterized by having comparatively small, ovate, more or less peltate leaves which are pale below and more or less pubescent or tomentose above and below. This is the most common variety and is pantropic in distribution. The latter variety has similar characteristics but differs in having a larger leaf, 4-9 cm. long and wide, which is obscurely peltate and rarely ovate. To avoid possible taxonomic confusion the remaining varieties will not be discussed as they have little or no bearing on the Panamanian flora. The synonomy for *Cissampelos pareira* has been restricted to American varieties for similar reasons.

MAGNOLIACEAE

By J. E. DANDY

Trees or shrubs, glabrous or with an indumentum of simple hairs; wood heteroxylous; branches annulate at the nodes with the scars of fallen stipules. Leaves alternate, stipulate, petiolate, simple; stipules large, free from the petiole or adnate to it, at first enclosing the young growths, later deciduous and leaving an annular scar round the node; lamina penninerved, entire or rarely 2- or more-lobed. Flowers terminal or axillary, usually solitary, pedunculate, actinomorphic, hermaphrodite or rarely unisexual, entomophilous, usually large and fragrant; peduncle bearing 1 or more deciduous spathaceous bracts which at first enclose the flower-bud and after falling leave annular scars. Perianth 2- or more-cyclic, 3-6-merous; tepals 6 or more, free, imbricate, usually subequal and fleshy but the outer whorl sometimes reduced in size or texture so as to simulate a calyx. Androecium of numerous free stamens spirally arranged; filaments short or more or less elongated; anthers linear, 2-thecous, introrse to extrorse, dehiscing by longitudinal slits; connective often produced above the anther-thecae into an appendage. Gynoecium superior, sessile or stipitate; carpels numerous to few (rarely 1), spirally arranged, free or sometimes concrescent; ovules 2 or more, biseriate on the ventral suture. Fruit apocarpous or sometimes syncarpous; fruiting carpels dehiscing longitudinally or more rarely circumscissile or indehiscent, sometimes samaroid. Seeds 1 or more in each fruiting carpel, large, suspended (when carpel dehiscent) by a silky thread; testa arilloid or sometimes adherent to the endocarp; endosperm copious, oily; embryo minute.

Species about 220, mostly in southeast Asia, the others in tropical America and southeastern North America. The two tropical American genera, *Magnolia* and *Talauma*, belong to the tribe Magnolieae and are both more strongly represented in Asia than in America. Some species of the Asiatic genus *Michelia* L., notably *M. champaca* L. and *M. figo* (Lour.) Spreng., are widely planted in the tropics; this genus is distinguished from *Magnolia* and *Talauma* by its axillary flowers with a stipitate gynoecium.

a. Carpels free, longitudinally dehiscent in fruit, the valves persistent; stipules free from the petiole, the latter therefore unscarred ..... 1. MAGNOLIA

aa. Carpels concrescent at least towards the base, woody and circumscissile in fruit, the upper portions falling away, the lower portions persistent and bearing the suspended seeds; stipules adnate to the petiole, leaving a scar on its upper surface ..... 2. TALAUMA

1. MAGNOLIA L.

MAGNOLIA L. Sp. Pl. 1: 535. 1753.

Evergreen or deciduous trees or shrubs. Stipules free from or adnate to the petiole. Flowers terminal, hermaphrodite, at first enclosed in 1 or more spathaceous bracts. Gynoecium sessile or shortly stipitate; carpels numerous or few, free; ovules 2, rarely 3-4 in the lower carpels. Fruiting carpels dehiscing longitudinally, the valves persistent.

Species about 80, the majority in southeast Asia, the others in tropical America and southeastern North America. The Panama species belongs to Sect. Theorhodon Spach, an American section which extends from the southeastern United States to the Greater Antilles and through Mexico and Central America to northern South America. This section differs from the other American sections in its free stipules. It includes *M. grandiflora* L., native of the southeastern United States, which is widely planted in the tropics. Many other species of *Magnolia* are cultivated in temperate gardens.

1. Magnolia sororum Seibert, in Ann. Missouri Bot. Gard. 25: 828. 1938.

Tree up to 30 m. tall; indumentum rufous or tawny; branchlets densely villous-pubescent when young. Leaf-lamina elliptic or ovate-elliptic to elliptic- or ovate-oblong, cuneate to obtuse or rounded at the base, obtuse to subacute or subacuminate at the apex, up to about 20 cm. long and 10 cm. broad, coriaceous, at first pubescent above on the midrib towards the base, densely pubescent beneath; lateral nerves about 10-14 on each side of the midrib; petiole up to about 3 cm. long, at first densely villous-pubescent, sometimes glabrescent; stipules villous-pubescent outside. Flowers very fragrant; bud ellipsoid; bracts 1-4, the uppermost or single one inserted immediately below the flower, densely villous-pubescent outside; peduncle stout, about 1.5-4 cm. long, densely villous-pubescent. Tepals 9, 3-merous, white; outer 3 obovate-oblong, about 4-7 cm. long, sparingly pubescent outside at the very base; inner 6 up to about 8 cm. long, glabrous. Stamens about 13-15 mm. long. Gynoecium ellipsoid; carpels about 20-45, densely villous-pubescent. Fruit ellipsoid to ellipsoid-oblong, about 4.5-6 cm. long; fruiting carpels shortly beaked.

Endemic to the mountains of western Panama, at 1100-2500 m. altitude. Hess reports the vernacular name *vaco* in Chiriquí.

Chiriquí: valley of the upper Rio Chiriquí Viejo, alt. 1300-1900 m., *White & White 21, 239;* vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 916;* vicinity of Casita Alta, north forested face of Cerro Copete, an eastern spur of Volcán de Chiriquí, alt. 2400-2550 m., *Allen 4874;* vicinity of Finca Lérida, alt. 1650 m. *Allen 4729;* Chiriquí, *Hess 261, 263.* Coclé: El Valle de Antón, crest of Cerro Pajita, alt. 1100 m., *Allen 3752.*

The handsome rufous or tawny indumentum readily distinguishes this species from the related *M. poasana* (Pittier) Dandy, which occurs to the west in Costa Rica.

2. TALAUMA Juss.

Talauma Juss. Gen. Pl. 281. 1789.

Svenhedinia Urb. in Fedde, Rep. Sp. Nov. 24: 3. 1927.

Evergreen trees or shrubs. Stipules adnate to the petiole. Flowers terminal, hermaphrodite, at first enclosed in 1 or more (usually several) spathaceous bracts. Gynoecium sessile; carpels numerous or few, concrescent at least towards the base; ovules 2. Fruiting carpels woody, circumscissile, the upper portions falling away

Figure 152. *Magnolia sororum*

either separately or in irregular masses, the lower portions persistent and bearing the suspended seeds.

Species about 45, mostly in tropical and subtropical southeast Asia, the others in tropical America in the Lesser Antilles, Cuba, southern Mexico and through Central America to Brazil. The genus is essentially tropical and lacks the strong North Temperate element present in *Magnolia*.

a. Leaves *rounded to obtuse at the apex, rather laxly reticulate* .....1. T. GLORIENSIS
aa. Leaves bluntly acuminate to subacute or apiculate at the apex, closely reticulate
2. T. SAMBUENSIS

1. TALAUMA GLORIENSIS Pittier, in Contrib. U.S. Nat. Herb. 13: 94. 1910
Magnolia allenii Standl. in Field Mus. Publ. Bot. 22: 331. 1940.

Tree up to 30 m. tall; branchlets glabrous. Leaf lamina ovate to ovate-elliptic or elliptic-oblong (occasionally obovate), cuneate to obtuse at the base, rounded to obtuse at the apex and sometimes slightly emarginate, up to about 31 cm. long and 16 cm. broad, coriaceous, glabrous; lateral nerves about 10-14 on each side of the midrib; petiole up about 5 cm. long, glabrous; stipules glabrous. Flower bud ovoid; bracts and peduncle glabrous. Tepals 9, 3-merous, greenish-white or creamy-white, glabrous; outer 3 oblong to oblong-elliptic, about 4-4.5 cm. long. Stamens about 13-15 mm. long. Gynoecium ovoid; carpels about 25-36, puberulous. Fruit ovoid; fruiting carpels up to about 4 cm. long, often becoming bifid at the apex.

Mountains of Costa Rica and western Panama, at about 1000 m. altitude. According to Pittier this species serves as a shade tree in the coffee plantations at La Gloria in the Cartago Province of Costa Rica.

COCLÉ: hills north of El Valle de Antón, alt. 1000 m., *Allen 2200, 3574.*

The Panama plant was described by Standley as a new species of *Magnolia, M. allenii;* his description was inaccurate in its reference to free stipules, connate bracts and glabrous carpels.

2. TALAUMA SAMBUENSIS Pittier, in Contrib. U.S. Nat. Herb. 20: 105. 1918.

Tree up to 40 m. tall; branchlets glabrous. Leaf lamina obovate- to elliptic- or ovate-oblong, cuneate to obtuse at the base, bluntly acuminate to subacute or apiculate at the apex, up to about 27 cm. long and 12.5 cm. broad, coriaceous or thinly coriaceous, glabrous; lateral nerves about 10-14 on each side of the midrib; petiole sometimes up to about 6 cm. long, glabrous; stipules glabrous. Flower-bud ovoid; bracts and peduncle glabrous. Tepals white. Fruit (according to Pittier) subglobose, about 8 cm. long and 7.5 cm. broad.

Endemic to southeastern Panama, at low altitudes up to 240 m.

DARIÉN: Río Cuasi, Chepigana District, alt. 240 m., *Terry & Terry 1420;* Boca de Pauarandó, on Río Sambú, alt. 20 m., *Pittier 5681.*

The available material of this species is too scanty for its characters to be fully described and understood. Its leaves are somewhat differently shaped at the apex and more closely reticulate than in *T. gloriensis*, which occurs further to the west and at a higher altitude.

WINTERACEAE

By J. E. DANDY

Trees or shrubs with homoxylous wood. Leaves alternate or sometimes subopposite or verticillate, exstipulate, simple; lamina penninerved, entire. Flowers terminal or axillary, solitary or in fascicles or simple or compound umbels, actinomorphic, hermaphrodite or unisexual. Perianth heterochlamydeous; calyx either closed round the bud and at length splitting into 2-3 lobes, or open and not enclosing the bud; petals 2-numerous (sometimes reduced to 1 or 0), free, imbricate. Stamens numerous or few, free, in 2 or more series; filaments more or less elongated; anthers small, 2-thecous, extrorse, dehiscing by longitudinal slits, the thecae parallel or convergent. Gynoecium superior, sessile or stipitate; carpels numerous or few (sometimes 1), in 1 or more series, free or sometimes concrescent; ovules several or numerous. Fruit apocarpous of 1 or more baccate carpels, or sometimes a syncarpous berry. Seeds with copious endosperm and a minute embryo.

An austral family of about 90 species, of which 4 are distributed in Central and South America, the remainder in the region of eastern Malaysia, the Solomon Islands, New Caledonia, Australia and New Zealand. The American species belong to the genus *Drimys* which is much more strongly represented in Malaysia and Australia.

1. DRIMYS J. R. & G. Forst.

Drimys J. R. & G. Forst. Charact. Gen. Pl. 83. 1776.

Wintera Murr. Syst. Veg. ed. 14, 507. 1784.

Trees or shrubs, sometimes epiphytic. Leaves alternate. Flowers hermaphrodite or unisexual, solitary, fasciculate or umbellate. Calyx at first completely closed round the bud, at length splitting into 2-3 often caducous lobes; petals 2 or more, sometimes reduced to 1 or 0. Carpels 1 or more, in 1 series, free; ovules 2-seriate on the ventral suture. Fruit apocarpous of 1 or more baccate carpels.

Species about 40, 4 in Central and South America, the others distributed in eastern Australia and in Malaysia from the Philippines and Borneo to New Guinea. The biggest concentration of species is in New Guinea.

1. Drimys granadensis L. f. Suppl. Pl. 269. 1781.

Wintera granadensis (L. f.) Murr. Syst. Veg. ed. 14, 507. 1784.

Shrub or small tree up to about 13 m. tall, glabrous. Leaf-lamina elliptic-oblong or narrowly elliptic-oblong to oblanceolate, cuneate or attenuate at the base, obtuse to rounded at the apex, up to about 17.5 cm. long and 5.5 cm. broad, coriaceous or subcoriaceous, glaucous or pale beneath; petiole up to about 2.5 cm. long. Flowers umbellate or fasciculate or sometimes solitary, hermaphrodite. Calyx 4.5-12 mm. long; petals 8-25, oblong to elliptic- or ovate-oblong, 5-25 mm. long. Stamens about 25-65, in 2-5 series. Carpels 3-24; ovules 7-12.

Southern Mexico to western Venezuela and Peru. The species is divided by A. C. Smith into five geographical varieties, the Panama population being regarded as endemic and named *D. granadensis* var. *chiriquiensis* A. C. Smith, in Journ. Arnold Arb. 24: 25. 1943; this variety occurs in rain-forest at about 1800-2250 m. altitude.

CHIRIQUÍ: Bajo Chorro, Boquete District, alt. 1800 m., *Davidson* 328.

Figure 153. *Drimys granadensis*

ANNONACEAE

By R. E. FRIES

Trees and shrubs with alternate and exstipulate leaves, always quite entire at the margins. Flowers generally trimerous. Sepals 3, valvate or imbricate. Petals generally 6, in two series, valvate or imbricate, free or rarely connate at the base, mostly conspicuously longer than the sepals; the inner petals often smaller, sometimes rudimentary or even absent. Stamens generally numerous; filaments short; anther cells adnate, the connective broad, usually expanded in a more or less truncate or hoodlike disc above the anther; the anther cells sometimes transversely septate by thin, horizontal membranes (anthers locellate). Carpels numerous, rarely few or solitary, generally free; ovules 1 or more. Fruiting carpels free (monocarps) or united in a dry or fleshy mass. Seeds with or without an aril, with copious ruminate endosperm; embryo minute.

This large family, which is of pantropic distribution, is represented in America by 36 genera. Two of them (*Annona* and *Xylopia*) occur also in Africa, two also in tropical Asia (*Artabotrys* and *Xylopia*). Only 14 genera and 41 indigenous species are recorded at present from Panama but there is no doubt that further investigations will show that more are to be found in the country.

Some species of *Annona* (in particular *muricata* L., *squamosa* L., *reticulata* L., and *Cherimolia* Mill.) are grown in the tropics for their edible fruits, and one or two of them are probably also cultivated in Panama. Only in respect to the last named, however, was any material from Panama available at the time when this was written. In the following, only the species known to grow wild in the Republic of Panama will be considered.

The Annonaceae of the Panama flora have been dealt with, *inter alia*, by Standley in his "Flora of the Panama Canal Zone" (in Contr. U.S. Nat. Herb. 27: 1-415. 1928) and "The Flora of Barro Colorado Island, Panama" (in Contr. Arnold Arboretum 5: 1-178. 1933). The first of these papers is very rich in valuable information on the native names of the species, for which readers are referred, as they are not quoted below.

a. Anthers not transversely septate.
  b. Petals not caudate-cuspidate.
    c. Flowers axillary.
      d. Petals imbricate.
        e. Connective of the stamens not expanded above the anther. 2. Oxandra.
        ee. Connective expanded into a truncate disk above the anther.
          f. Ovule attached close to the upper end of the ovary and pendulous, sometimes located lower down, but not basal; pedicel nearly always with a small bract above the articulation ..... 1. Cremastosperma.
          ff. Ovule basal, erect; pedicel without a bract above the articulation ..... 3. Guatteria.

dd. Petals valvate.
e. Petals not keeled on the inner surface; ovules lateral, usually few to several, rarely solitary and, if so, attached near the lower or upper end of the ovary; monocarps irregularly bursting .....4. Unonopsis
ee. All petals, or only the inner, keeled on the inner surface above the middle; ovules 2, erect, basal; monocarps opening on the inside by a longitudinal split .....6. Anaxagorea.
cc. Flowers not axillary, more or less opposite the leaves.
d. Petals imbricate.
e. Pubescence of simple hairs; monocarps stipitate, free....9. Malmea.
ee. Pubescence of stellate hairs or stellate scales; monocarps sessile, often concrete .....12. Duguetia.
dd. Petals, at least the outer, valvate.
e. Monocarps free, stipitate .....7. Desmopsis.
ee. Monocarps sessile, united into a dry or fleshy mass.
f. Outer petals without wings or spurs .....13. Annona.
ff. Outer petals produced into wings or spurs .....14. Rollinia.
bb. Petals long caudate-cuspidate; ovules lateral .....8. Stenanona.
aa. Anthers transversely septate.
b. Pedicels with bracts .....5. Xylopia.
bb. Pedicels entirely without bracts.
c. Petals not saccate .....10. Porcelia.
cc. Inner petals large, saccate, with involute margins .....11. Cymbopetalum.

1. CREMASTOSPERMA R. E. Fries

Cremastosperma R. E. Fries, in Acta Hort. Berg. 10:46. 1930; 11: 323. 1931.

Shrubs or trees with 1, rarely 2, axillary flowers, or sometimes cauliflorous. Flowers medium-sized, generally glabrous; pedicels articulate above the base, nearly always with one small bract above the articulation. Sepals free, imbricate in bud, with thin, ciliolate margins. Petals much longer than the calyx, rigid, imbricate, with thin edges. Stamens numerous, the connective expanded above the anther into a disk. Carpels several; ovule 1, attached close to the upper end of the ovary and pendulous, or sometimes located lower down, even near the base and then erect. Monocarps free, stipitate, 1-seeded.

Seventeen species are known, inhabiting the most tropical parts of South America, from Panama and Colombia to Peru, Bolivia, Amazonian Brazil and French Guiana. Only one species is known from Panama.

Cremastosperma anomalum R. E. Fries, Svensk. Vet.-Akad. Handl. ser. 3, 24^{10}: 4, *pl. 1 c-d.* 1948.

Tree up to 10 m.; young branchlets glabrous, reddish. Leaves on petioles 5-8 mm. long, quite glabrous and lustrous on both sides, elliptic or oblong and broadest at the middle, rotundate at the base, abruptly cuspidate at the apex, (10-)15-28 cm. long and 5-10 cm. broad. Flowers solitary, white but blackening when dried; pedicels quite glabrous, 1-2 cm. long, articulate, without any bract above the articulation. Sepals glabrous, connate into a disk 8-10 mm. broad with ciliolate margin. Petals orbicular, 1.5 cm. diam., very shortly sericeous-tomentellous. Stamens

Figure 154. *Cremastosperma anomalum*

few, 2.0-2.5 mm. long. Carpels very numerous; ovule 1, attached near the base of the ovary, erect. Monocarps ellipsoid, 15-18 mm. long and 8 mm. across, black.

Panama and Colombia.

DARIÉN: vicinity of El Real, ca. 15 m. *Allen 969;* near the mouth of Río Yape, ca. 20 m., *Allen 348.*

2. OXANDRA A. Rich.

Oxandra A. Rich. in Sagra, Cub. 10: 45. 1845; R. E. Fries, in Acta Hort. Berg. 10: 153. 1931.

Trees or shrubs. Flowers small, solitary in the axils or in few-flowered axillary inflorescences; pedicels articulate a little above the base, bearing a few small, distichous bracts below and 1 above the articulation. Sepals 3, connate at the base, imbricate in bud, persistent. Petals 6, thin, black when dried, all rather alike, orbicular, ovate or oblong, imbricate. Receptacle hemispheric. Stamens 6-20, lanceolate-oblong, the connective elongated above the anther into a triangular to lanceolate appendage. Carpels rather few, (1-)4-13; ovaries cylindric-ovoid; stigma sessile, capitate or shortly clavate; ovule 1, basal, erect. Monocarps free, nearly sessile or shortly stipitate, 1-seeded. Seeds without an aril.

A rather large genus with 23 species in tropical America, distributed from the West Indies and Panama to southern Brazil; only 2 species are recorded from Panama.

a. Leaves lanceolate, acute at the base ..... 1. O. panamensis.

aa. Leaves elliptic or oblong-elliptic, rounded at the base ..... 2. O. longipetala.

1. Oxandra panamensis R. E. Fries, in Acta Hort. Berg. 10: 168, *fig.* 5, *c*, 1931.

Tree up to 6 meters high; young branchlets covered with crisp hairs. Leaves on petioles 3-5 mm. long, finally glabrous on both sides, but densely verruculose beneath and thinly appressed-hairy on the midrib beneath, lanceolate, broadest at the middle and equally narrowed and acute at both ends, 8-12 cm. long and 2.0-3.5 cm. broad. (Flowers unknown). Fruits on very short rigid pedicels (2-3 mm.); monocarps glabrous, black when dried, ellipsoid, 12-15 mm. long and 9-10 mm. across; stipes 1-1.5 mm. long.

Darién: Marraganti and vicinity, 10-200 ft., *Williams 1017;* Boca de Cupe, *Williams 669.*

2. Oxandra longipetala R. E. Fries, in Acta Hort. Berg. 10: 170, *pl.* 5. 1931.

A small tree; young branchlets hirsute-tomentose. Petioles very short (about 1 mm. long). Leaves glabrous on the upper side, the midrib tomentellous when young, glabrous beneath and sparsely appressed-hairy on the midrib, elliptic or oblong-elliptic, rotundate and even subcordate at the base, rather long-acuminate at the obtuse apex, 7-10 cm. long and 2.5-3.5 cm. broad. Flowers solitary; pedicels 5-6 mm. long, appressed-hairy; flower buds oblong. Sepals rotundate-ovate. Petals linear-oblong, rotundate at the apex, up to 16 mm. long. Carpels about 11. (Fruit unknown).

Canal Zone: near Salamanca Hydrographic Station in the gorge of the R. Pequení, 70-80 m., *Dodge, Steyermark & Allen 16968;* Lion Hill Station, *Hayes*, 385.

Figure 155. *Oxandra longipetala*

3. GUATTERIA Ruiz & Pav.

GUATTERIA Ruiz & Pav. Fl. Peruv. & Chil. Prodr. 85, *tab. 17.* 1794; R. E. Fries, in Acta Hort. Berg. 12: 291. 1939.

Shrubs or trees, rarely climbing; the pubescence of simple hairs. Flowers axillary, solitary or in few-flowered inflorescences; pedicels articulate, with a few small bracts (rarely foliaceous) below the articulation, no bracts above this. Sepals valvate. Petals imbricate, usually hairy, especially so outside at the base. Stamens numerous; connective expanded above the anther into a truncate disc; anther cells not locellate. Carpels numerous; ovule 1, basal, erect. Monocarps ovoid or ellipsoid, or shortly cylindrical-ellipsoid, 1-seeded, stipitate or rarely almost sessile. Seeds without an aril.

The genus is the largest in the family Annonaceae, the species numbering about 240. It is distributed from southern Mexico and the West Indies to Bolivia and southern Brazil, centering in the Amazonian region and Guiana.

a. Leaves not verrucose.
  b. Pubescence appressed.
    c. Leaves 3-5 cm. broad ..... 1. G. LUCENS
    cc. Leaves broader than 6 cm.
      d. Leaves rounded and a little emarginate at the base ..... 2. G. AMPLIFOLIA
      dd. Leaves acute at the base.
        e. Petals oblong, all of about the same length ..... 3. G. INUNCTA
        ee. Petals broadly ovate to orbicular, the inner shorter.
          f. Petioles 1.0-1.5 cm. long, the upper half narrowly winged; lateral nerves elevated on the upper side of the leaves ..... 4. G. SLATERI
          ff. Petioles 3-7 cm. long; lateral nerves impressed on the upper side ..... 5. G. PANAMENSIS
  bb. Pubescence spreading.
    c. Leaves oblanceolate to obovate; flower pedicels 8-10 mm. long. .... 6. G. ALLENII
    cc. Leaves linear-oblong; flower pedicels about 20 mm. long .... 7. G. CHIRIQUIENSIS

aa. Leaves very verrucose on both sides.
  b. Branchlets, pedicels and under side of the leaves with spreading pubescence; leaf-petioles 1-2 mm. long ..... 8. G. AERUGINOSA
  bb. Branchlets, pedicels and under side of the leaves with appressed pubescence; leaf-petioles 6-8 mm. long ..... 9. G. DUMETORUM

1. GUATTERIA LUCENS Standl. in Trop. Woods 42: 22. 1935; R. E. Fries, in Acta Hort. Berg. 12: 481, *pl.* 34. 1939.

A small tree, the young branchlets sparsely sericeous, soon glabrous and blackening. Leaves with petioles 6-8 mm. long, lustrous on both sides, finally glabrous above except on the more or less hirsute midrib, sparsely appressed-hairy beneath, oblong-lanceolate, acute and decurrent at the base, tapering at the apex into an acumen 1-2 cm. long, 10-16 cm. long and 3.5-4.5 cm. broad. Flowers 1 or 2 in the axils of persistent or newly fallen leaves; pedicels thin, rigid, black, sparsely sericeous, glabrescent, 10-13 mm. long, articulate 3-4 mm. above the base. Sepals rounded-ovate, about 2.5 mm. long. Petals green but blackening when dried, puberulous, sericeous outside at the base, oblong-spathulate, rounded at the apex,

Figure 156. *Guatteria amplifolia*

the outer up to 12 mm. long and 4 mm. broad, the inner a little larger. Stamens 1 mm. long, connective disc very shortly setulose. (Fruits unknown).

SAN BLAS: Permé, *Cooper 280.*

2. GUATTERIA AMPLIFOLIA Tr. & Pl. in Ann. Sc. Nat., sér. 4. 17: 35. 1862; R. E. Fries, in Acta Hort. Berg. 12: 376, *fig. 12, a.* 1939.

Branchlets glabrous. Leaf petioles 4-5 mm. long, rugose, glabrous; blades papyraceous, glabrous above, sparsely provided beneath with very short appressed hairs, elliptic or oblong-elliptic or ovate, rotundate and a little emarginate at the very base, more or less abruptly cuspidate, 20-40 cm. long and 7-12 cm. broad; lateral nerves 18-25 on each side, more or less impressed on the upper side. Flowers solitary or sometimes 2; pedicels sericeous, 1-1.5 cm. long. Sepals triangular-ovate, reflexed, sericeous outside, tomentellous inside, 6-8 mm. long. Petals ferruginous-tomentellous on both sides, oblong-lanceolate, finally oblong-obovate, rotundate at the apex, 15-18 mm. long, 8-12 mm. broad. Stamens 1.8 mm. long. Monocarps ellipsoidic-pyriform, rugose, apiculate, 8-9 mm. long and 5 mm. across; stipes 10-15 mm. long, rigid.

CANAL ZONE: Chagres, *Fendler 3;* Lion Hill Station, *Hayes 346;* shores of Gatún Lake, *Bangham 464;* Barro Colorado Island: Barbour Point, *Shattuck 406,* and Chapman Trail, *Starry 170,* and Barbour-Lathrop Trail, *Starry* 325.

3. GUATTERIA INUNCTA R. E. Fries, in Acta Hort. Berg. 12: 378. 1939.

Guatteria Ouregou Griseb. Fl. Brit. W. Ind. 7.1860, pro parte quoad specimen a St. Thomas citatum, non Dunal.

A shrub or tree up to 8-10 m. high, young branchlets at first shortly ferruginous-sericeous. Leaves on petioles 5-8 mm. long, chartaceous, pale green and soon quite glabrous above, under side olivaceous and densely appressed-hirsute at first, finally nearly glabrous, elliptic to oblong-elliptic, broadest at the middle, acute and a little decurrent at the base, rather gradually tapering to the blunt apex, 15-28 cm. long and 6-12 cm. broad. Flowers 1-2; pedicels very thin but rigid, 1.5-2.0 cm. long. Sepals rotundate-ovate, ferruginous-sericeous outside, glabrous inside, 4-5 mm. long. Petals oblong and rotundate-truncate at the apex, ferruginous-sericeous outside, 10-15 mm. long, 5-8 mm. broad. Stamens 1.3-1.5 mm. long. Monocarps ellipsoidic, very shortly apiculate at the apex, acute at the base, about 7 mm. long and 4 mm. across; stipes thin, about 7 mm. long.

Costa Rica and Panama.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Water Valley, *Von Wedel 1460, 1716;* Old Bank Island, Isla Colón, alt. 0-120 m., *Von Wedel 1932.*

GUATTERIA INUNCTA, var. CAUDATA R. E. Fries, in Ann. Missouri Bot. Gard. 42: 152. 1955.

Differs from the type in the leaves, relatively narrower, narrowly cuneate at the base, with a narrowly caudiform apical acumen 2.0-3.5 cm. long, and in the more slender pedicels of the flowers.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Old Bank Island, *Von Wedel 2108.*

4. GUATTERIA SLATERI Standl. in Field Mus. Publ. Bot. 4: 206. 1929; R. E. Fries, in Acta Hort. Berg. 12: 517. 1939.

Tree up to 10 m. high, the young branchlets ferruginous-sericeous. Leaf petioles 1.0-1.5 cm. long, the upper part narrowly winged; blades blacken when drying, glabrous on upper side from the first, with sparse short appressed hairs beneath (longer on the midrib) and more or less glabrescent, elliptic to obovate, acute and long-decurrent at the base, rather abruptly contracted into an obtuse cusp 1-2 cm. long, 15-20 cm. long and 5-8 cm. broad. Flowers solitary, pedicels 1.5-2.0 cm. long, rigid. Sepals rotundate-ovate, about 4 mm. long and broad, soon recurvate, deciduous, sericeous outside, glabrous inside. Petals broadly ovate, rotundate at the apex, 8-12 mm. long and broad, golden yellow-sericeous outside, tomentellous inside, the inner a little smaller. Stamens 1.2-2.0 mm. long.

CHIRIQUÍ: Progreso, *Cooper & Slater, 177;* Bajo Chorro, Boquete District, in rain forest, alt. 6000 ft., *Davidson 233;* Boquete Region, Cerro Horqueta, cloud forest, alt. 6500 m., *Von Hagen & Von Hagen 2135.* BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, alt. 6000-7000 ft., *Allen 4802.*

5. GUATTERIA PANAMENSIS R. E. Fries, in Arkiv Bot. andra ser. 1: 335. 1950.

Guatteria costaricensis subsp. *panamensis* R. E. Fries, in Acta Hort. Berg. 12: 515. 1939.

A tree 10-15 m. high; branchlets ferruginous-sericeous. Leaves on petioles 3-7 mm. long, membranaceous, more or less blackening when dried, smooth above and hirsute at first at the midrib but soon quite glabrous, with appressed rigid hairs beneath, finally presumably glabrous, oblong or oblong-obovate, broadest at the middle or a little above the middle, acute at the base, abruptly contracted into a broad obtuse cusp 1 cm. long, 20-28 cm. long and 6-9 cm. broad. Flowers solitary or 2 in the axils of persistent or fallen leaves; pedicels sericeous, about 3 cm. long. Petals finally horizontally expanded, ovate and rotundate at the apex, the outer densely sericeous outside, tomentellous on the upper half inside, about 1 cm. long, the inner tomentellous outside and glabrous inside, a little smaller than the outer. Monocarps very numerous, ellipsoid to obovoid, shortly acute, 9-10 mm. long and 5.0-5.5 mm. across, abruptly tapering into a thin stipe 5-7 mm. long.

Known only from Panama.

BOCAS DEL TORO: region of Almirante, Daytonia Farm, *Cooper 382;* Old Bank Island vicinity of Chiriquí Lagoon, *Von Wedel 1965.*

6. GUATTERIA ALLENII R. E. Fries, in Arkiv Bot. andra ser. 1: 336. 1950.

A tree about 12 m. high; young branchlets very densely covered with rigid ferruginous erect-patent hairs. Leaves on petioles 2-3 mm. long, membranaceous, glabrous above except on the more or less tomentose midrib, pale green beneath and rather thinly clothed with decumbent or patent hairs, more densely along the thicker nerves, oblanceolate-obovate, tapering into a cuneate acute base, abruptly contracted at the apex into an acumen 0.5-1.0 cm. long, 10-18 cm. long and 3-7 cm. broad. Flowers solitary in the axils; pedicels thick, 8-10 mm. long, articulate about 2 mm. above the base. Sepals rotundate, about 4 mm. long and broad. Petals oblong, tapering towards the blunt apex, densely golden-sericeous on the outside, especially near the base, 10-15 mm. long and 5-6 mm. broad. Stamens with connectives 1.5 mm. long, disk velutinous. (Fruit unknown).

COCLÉ: north rim of El Valle, *Allen 1900.*

7. GUATTERIA CHIRIQUIENSIS R. E. Fries, in Svensk. Vet-Akad. Handl. ser. 3. 24^{10}: 11. 1948.

Young branchlets shortly ferruginous-hirsute. Leaf petioles 1-3 mm. long; blades glabrous above except on the densely tomentose midrib, underside rather sparsely clothed with patent ferruginous persistent hairs, linear-oblong, acute and shortly decurrent at the base, rather abruptly contracted into an obtuse cusp about 1.5 cm. long. Flowers solitary (or more?), their pedicels about 2 cm. long, rigid, articulate about 5 mm. above the base, the lower part sericeous, the upper provided with more patent ferruginous hairs. Sepals broadly ovate, acute, ferruginous-sericeous outside, glabrous inside, about 5 mm. long. Petals thick, horizontally expanded, elliptic-oblong and rotundate at the apex, densely golden-sericeous

outside, subglaucous inside, pulverulent upwards on both sides. Stamens 1.7-2.0 mm. long. Monocarps black, narrowly ellipsoidic-clavate, 9-10 mm. long and 4-5 mm. broad on stipes 6-7 mm. long.

CHIRIQUÍ: vicinity of San Félix, alt. 0-120 m., *Pittier 5132, 5748.*

8. GUATTERIA AERUGINOSA Standl. in Field Mus. Publ. Bot. 4: 206. 1929.

Tree about 15 m. high; young branchlets densely clothed with short ferruginous hairs. Leaves on very short petioles (1-2 mm. long), 14-18 cm. long and 4-5.5 cm. broad, oblong to oblanceolate and broadest above the middle, shortly narrowed to the base, long-cuspidate at the apex, verruculose-punctate on both sides, ferruginous-pilose on the midrib above and finally glabrous, densely rubiginous-pilose beneath, later thinly ferruginous-hirsute, the hairs rather long-patent and soft. Flowers solitary; pedicels thick, rigid, densely pilose, 1-3 cm. long, articulate 3-4 mm. above the base, Petals thick, finally horizontally expanded, sericeous-tomentellous on the outside, tomentellous on the inside except at their glabrous base, ovate to oblong-elliptic, the outer petals up to 13 mm. long and 6-8 mm. broad, the inner a little shorter. Stamens 1.5-1.7 mm. long. Monocarps black, narrowly ellipsoid, acute at both ends, 10 mm. long and 4 mm. across.

BOCAS DEL TORO: *Von Wedel 155, 490;* Isla Colón vicinity of Chiriquí Lagoon, *Von Wedel 2856;* Cricamola, near Almirante, *Cooper 526, 526a.*

9. GUATTERIA DUMETORUM R. E. Fries, in Svensk. Vet.-Akad. Handl. ser. 3, 24^{10}: 12. 1948.

Young branchlets appressed-hairy, glabrescent. Leaf petioles 6-8 mm. long; blades densely verrucose on both sides, hirsute at first above but soon quite glabrous, underside covered at first with long more or less ferruginous appressed hairs, finally nearly glabrescent but still with some hairs especially on the midrib, oblanceolate, gradually tapering and decurrent at the base, rather abruptly contracted at the apex into an obtuse acumen 1-1.5 cm. long, about 15 cm. long and 4-5 cm. broad. Flowers 1-2 in the axils of leaves; pedicels thin, sparsely sericeous, about 2 cm. long, articulate about 0.5 cm. above the base. Sepals finally recurvate, ovate, acute, densely sericeous outside, glabrous inside, 3-4 mm. long. Petals oblong to rhombic-ovate, narrowed to the obtuse apex, 10 mm. long and 4-5 mm. broad, flavescent-tomentellous outside; outer petals pubescent at the base, inner petals with longer appressed golden-yellow hairs nearly up to the apex. Stamens 1 mm. long, the connective disk plane, glabrous. (Fruit not known).

COLÓN: along Río Fató, in forests and thickets, alt. 10-100 m., *Pittier 3915.*

4. UNONOPSIS R. E. Fr.

UNONOPSIS R. E. Fries, in Svensk. Vet.-Akad. Handl. 34^{5}: 26. 1900.

Shrubs or small to medium-sized trees. Inflorescences axillary or sometimes produced from older branches or from the trunk; pedicels articulate above the basal bract and provided with a second bract above the articulation. Flowers small, the

buds spherical. Sepals minute, valvate. Petals rigid, valvate, ovate or rotund, concave, the inner thick in particular; pollen sacs not locellate; connective expanded above the anther into a truncate disk. Carpels several to numerous; ovules (up to 6-8), lateral, or else solitary and attached near the lower or upper end of the ovary. Monocarps free, stipitate.

A large genus of about 30 species, inhabiting a vast area from British Honduras and the West Indies to south Brazil; only 2 species recorded from Panama.

a. Leaves elliptic to obovate-elliptic, 20-30 cm. long; pedicels thin, 2-4 cm. long; ovules solitary .....1. U. PITTIERI.

aa. Leaves oblong-oblanceolate, 15-20 cm. long; pedicels short and thick (circ. 7 mm. long—or more?); ovules 3-4, lateral .....2. U. PANAMENSIS

1. UNONOPSIS PITTIERI Saff. in Journ. Washington Acad. Sci. 15: 102. 1925.

Trees of moderate size, 10 m. tall, with pyramidal crown; young branches minutely sericeous, becoming glabrous and blackish, densely lenticellate, the stouter with grayish bark. Leaf petioles at first puberulent, becoming glabrous and blackish, 3-5 mm. long, flat or channelled above; blades membranaceous-papyraceous, almost concolorous, at first sericeous on both sides but soon glabrescent, beneath with some more or less persistent hairs along the midrib or completely glabrous, the whole surface finely verruculose-punctate, elliptic or obovate-elliptic, narrowed toward the base and broadly acute or obtusish, cuspidate at the tip, 20-30 cm. long and 5-9 cm. broad, the veins on both sides prominent, 12-15, arcuate, irregularly gathered toward the margin. Inflorescences on leafless branches, about 1 cm. thick; pedicels thin, minutely sericeous, 2-4 mm. long, articulate about midway and bearing a minute bracteole. Sepals 1.5 mm. long, sericeous without, triangular and strongly connate. Petals valvate, broadly ovate, acute, the outer rather thick, glaucous-sericeous without, about 9 mm. long and 7 mm. broad, the inner thicker, 5-6 mm. long and 4-5 mm. broad, the midrib sericeous without but otherwise glabrous. Stamens 1.5 mm. long. Pistils 14-18, the ovaries cylindric-prismic, glabrous save the hairy angles, 1.5-1.7 mm. long, the stigmas conic-ovoid, 1 mm. long, the ovules solitary, attached below midway, horizontal. Monocarps brown, globose, 11-12, glabrous, with a stipe about 1 cm. long.

CANAL ZONE: headwaters of Rio Chinilla, above Nuevo Limón, *Maxon 6890*. COLÓN: along the Río Fató, in forests or thickets, alt. 10-100 m., *Pittier 3871*.—Also reported by Standley from Barro Colorado Island.

This species occurs also in Costa Rica, from whence the very closely related *U. schippii* is described.

2. UNONOPSIS PANAMENSIS R. E. Fries, in Ann. Missouri Bot. Gard. 42: 151. 1955.

Young branches with short ferruginous erect or appressed hairs. Leaf petioles terete or flattened above, tomentellous, 4-5 mm. long; blade chartaceous, above glabrous save for the minutely hairy glabrescent midrib, beneath hirsute-glabrescent along the midrib, oblong-oblanceolate, broadest above the middle, shortly acute at the base, abruptly contracted at the tip with a cusp 1.0-1.5 cm. long, 15-20 cm. long and 4-5 cm. broad, the midrib elevated on both sides, the stronger veins

Figure 157. *Unonopsis panamensis*

about 15 on both sides, arcuately ascending and converging about 1-2 mm. from the margin, slender and prominent above. Inflorescences springing from the axils of fallen leaves; pedicels thick, ferruginous-sericeous, 7 mm. long or longer, articulated slightly above the base. Sepals free, rotund-ovate, acutish, about 2 mm. long. Petals stiff, blackening in desiccation, the outer rotund, about 7 mm. in diameter and ferruginous-sericeous without, the inner smaller, ferruginous-tomentose along the midrib. Stamens 1.8-2.0 mm. long, truncate at the tip. Ovaries 1.5 mm. long, prismatic and shortly strigose, tipped with a globose-ovoid stigma; ovules 3-4, lateral. (Fruit unknown.)

Known only from Panama.

PANAMÁ: Cerro Campana, trail from Campana to Chica, alt. 600-800 m., *Allen 2647*.

5. XYLOPIA L.

XYLOPIA L. Syst. ed. 10. 1759; R. E. Fries, in Acta Hort. Berg. 10: 85. 1930.

Shrubs or trees. Flowers usually small, sessile or shortly pedicellate, in axillary inflorescences or sometimes produced from old branches or from the trunk. Sepals small, valvate in bud, nearly free or connate into a cupular calyx. Petals thick, valvate, linear-oblong or sometimes deltoid. Stamens numerous, the anther cells locellate; connective expanded above the anther. Ovaries hidden in a deep cavity in the center of the torus; ovules lateral. Monocarps free, cylindric or sometimes short, clavate, containing a row of rather few seeds.

About 50 species in America, distributed from Central America and the West Indies to southern Brazil and Paraguay; also in the tropics of the Old World. Only 4 species are known at present from Panama.

a. Sepals nearly free or connate up to the middle; carpels few (4-8).
  b. Flowers numerous in axillary inflorescences; flower buds elongate, cylindric-trigonous; petals linear-oblong ..... 1. X. FRUTESCENS.
  bb. Flowers solitary; flower buds ovoid; petals flat, the outer ovate..... 2. X. BOCATORENA.

aa. Calyx cup-shaped with almost wholly connate sepals; carpels numerous (25-45).
  b. Flowers numerous in axillary inflorescences; flower buds narrowly cylindric-trigonous; outer petals 2-3 mm. broad ..... 3. X. AROMATICA
  bb. Flowers solitary, axillary; flower buds thick, cylindric; outer petals about 8 mm. broad ..... 4. X. MACRANTHA.

1. XYLOPIA FRUTESCENS Aubl. Pl. Guy. Fr. 1:602, *t.* 292. 1775, excl. syn. Linn. et Brownei.

Xylopia setosa Poir. in Lam. Encycl. Méthod. 18: 812. 1808.

Xylopia muricata Vell. Fl. Flumin. 9: *t. 127*. 1827; non Linn.

A medium-sized tree or shrub; young branchlets densely covered with about 2 mm. long, more or less ferruginous, erect-patent hairs. Leaves rigid, glabrous on upper side, densely covered underneath with long appressed hairs, lanceolate, acute at the base, rather long-acuminate, 4-6 cm. long and 0.8-1.5 cm. broad; petioles 2-4 mm. long. Inflorescences 1-5-flowered, axillary. Sepals ovate, about 2 mm. long,

Figure 158. *Xylopia frutescens*

shortly connate at the base. Outer petals 8-11 mm. long and 2.5 mm. broad, oblong-obtuse, sericeous; inner petals a little shorter and narrower. Carpels 6 (or more ?); style with stigma 4 mm. long, glabrous, curvate and thickened above the base. Monocarps 10-13 mm. long and 9-10 mm. broad, rhomboid-globose, obtuse, contracted at the base into a stipe 1-2 mm. long. Seeds 2 (or 1), ovoid, black, 6-7 mm. long.

Distributed from Central America (Guatemala and British Honduras) to southern Brazil (Rio de Janeiro and Minas Geraës).

CANAL ZONE: low hill north of Balboa, *Gillespie P 33;* Barro Colorado Island, *Shattuck* 250. PANAMÁ: Sabana, *Pittier* 2539 Panamá, *Haenke 167, Seeman s.n.;* vicinity of Arraiján, *Allen 1765;* Isthmus of Panamá, in woods, *Hayes 670;* Punta Paitilla, *Piper 5410;* vicinity of Juan Franco Race Track, *Standley 27760.*

2. XYLOPIA BOCATORENA Schery, in Ann. Missouri Bot. Garden 30:86. 1943.

Tree, its young branchlets very shortly and densely tomentellous. Leaves rigid, on petioles 2-3 mm. long, elliptic-lanceolate, acute at the base, long acuminate at the apex, glabrous above, thinly provided beneath with short appressed hairs, 8-11

cm. long, and 2.3-3.5 cm. broad. Flowers solitary; pedicels sericeous, often recurved, 5-6 mm. long; flower buds ovoid, about 1 cm. long. Sepals connate up to the middle. Petals flat; the outer ovate, sericeous outside, about 12 mm. long and 6 mm. broad; the inner rhombic-lanceolate, 11 mm. long and 4-5 mm. broad. Stamens 3 mm. long, connective appendage ellipsoid. Carpels about 8. Monocarps 1-4 (or more), obovoid to clavate, ca. 2 cm. long. Seeds 2, black.

BOCAS DEL TORO: Isla Colón, vicinity of Chiriquí Lagoon. *Von Wedel 2965.*

3. XYLOPIA AROMATICA (Lam.) Eichl. in Mart. Fl. Bras. 13[1]: 43. 1841; R. E. Fries, in Acta Hort. Berg. 10: 106. 1930 (where 23 synonyms are quoted).

A tree; young branchlets tomentose. Leaves large, 8-15 cm. long and 2.0-4.5 cm. broad, rigid, lanceolate or elliptic-lanceolate, gradually narrowing at the apex, rounded or shortly acute at the base, glabrous on the upper side from the first except on the midrib, covered underneath with short patent or appressed hairs or even glabrous, glaucous; petioles 3-6 mm. long. Flowers numerous in axillary inflorescences; flower buds long and narrow, trigonous, densely sericeous. Calyx cup-shaped, with almost wholly connate sepals. Outer petals linear, up to 30 mm. long and 2-3 mm. broad; inner petals a little shorter, about 1 mm. broad. Stamens 1.0-1.5 mm. long. Carpels very numerous (about 25). Monocarps cylindric, torulose, 2.0-2.5 cm. long and 6-7 mm. thick. Seeds about 6, ovoid, black, 5-6 mm. long.

This is the most widely distributed species of all American Xylopias, covering a large area from Central America and the West Indies down to southern Brazil and Paraguay.

PANAMÁ: sabanas near Chepo, 30 m., *Hunter & Allen 49;* Río Tataré, *Woodson & Schery 1018;* Isla Taboga, ca. 0-186 m, *Woodson, Allen & Seibert 1447;* Bohio, *Pittier 3417;* savanas north of Panamá city, *Brother Paul 443;* Island San José in sinu Panamensi, *Andersson s.n.*

4. XYLOPIA MACRANTHA Tr. & Pl. in Ann. Sc. Nat., sér. 4. 17: 38. 1862. R. E. Fries, in Acta Hort. Berg. 10: 112, *fig.* 8. 1939.

Young branchlets sericeous-villous. Leaves 3-4 mm. long, petiolate, coriaceous, glabrous and lustrous above, covered beneath with long appressed hairs, finally glabrescent, oblong, rounded at the base, gradually narrowed into an obtuse apex, 9-12 cm. long and 3-4 cm. broad. Flowers solitary in the axils of fallen leaves; pedicels thick, 5-6 mm. long. Sepals nearly wholly connate, forming a cup 8-10 mm. high and 10-11 mm. broad, ferruginous-sericeous on the outside. Petals thick, rigid, ligneous, 20-23 mm. long, the outer plane, oblong, sericeous on the outside, grey-tomentellous on the inner side, 8 mm. broad; inner petals quadrangular-prismatic, very acute, about 3 mm. in diameter, broadened at the base. Stamens 1.5-2 mm. long. Carpels numerous (about 45). Fruit unknown.

At first described from Colombia, but later found in many localities in Panama and Venezuela.

CANAL ZONE: along Caño Quebrado, *Pittier 6822;* Barro Colorado Island in Gatún Lake, alt. 120 m. or less, *Standley 41085;* hills north of Frijoles, *Standley 27483;* hills west of the Canal, near Gatún, *Standley 27211;* Barbour Point, *Bangham 490;* end of Van Tyne Trail, Barro Colorado Island, *Zetek 3903.* COLÓN: vicinity of Camp Pina, *Allen 3676.*

6. ANAXAGOREA St. Hil.

ANAXAGOREA St. Hil. in Bull. Soc. Philom. Paris 91. 1825; R. E. Fries, in Acta Hort. Berg. 12: 6. 1934.

Small trees or shrubs. Flowers small, axillary, sometimes produced on the older, leafless branches; pedicels bracteolate. Sepals thin, valvate in bud, free or sometimes connate at first and irregularly splitting, often deciduous. Petals valvate, all rather alike, but the inner mostly a little smaller and thicker, all, or only the inner, keeled on the inner surface above the middle. Stamens several, the innermost often sterile; connective of the fertile stamens not forming a disk above the pollen sacs, elongated into a ligule, sometimes very short. Carpels several; ovules 2, erect, produced from the basal part of ovary cavity. Monocarps free, dry, stipitate, club-shaped, opening along the inner sides. Seeds 2, very smooth and lustrous, appressed against each other and therefore plane on one side side and convex on the other.

A rather large genus, containing 20 American species occupying a vast region from Central America and Colombia to southern Brazil, centering along the Amazon.

a. Leaves smaller (8-16 cm. long), acute and long-decurrent at the base; the secondary nerves 7-8 per side ..... 1. A. PANAMENSIS.

aa. Leaves larger (30-35 cm. long), rounded at the base; the secondary nerves about 15 per side ..... 2. A. ALLENII.

1. ANAXAGOREA PANAMENSIS Standl. in Journ. Washington Acad. Sc. 15: 101. 1925; R. E. Fries, in Acta Hort. Berg. 12: 24. 1934.

A shrub up to 2 m. high; the young branchlets minutely ferruginous-puberulous, soon glabrescent. Leaves on petioles 4-7 mm. long, membranaceous, paler and puberulous beneath, finally glabrous on both sides, lanceolate-oblong, acute and decurrent at the base, rather gradually tapering at the apex, 8-16 cm. long and 3.0-4.5 cm. broad; secondary nerves 7-10 per side. Flowers solitary; pedicels 2.0-2.5 cm. long, finally glabrous, provided near the calyx with an orbicular, amplectant bract, 1 mm. long. Sepals membranaceous, ovate, acuminate, ferruginous-puberulous, 8 mm. long. Outer petals linear-oblong, obtuse, 2 cm. long; inner petals triangular-ovate, acuminate, ca. 1 cm. long. Monocarps glabrous but rugose, apiculate at the apex, 2.2-2.5 cm. long, together with the stipe.

PANAMÁ: in wet forest along the Río Tapía, near sea-level, *Standley 26168.*—According to Standley also collected on the hills north of Frijoles, Canal Zone: *Standley 27589.*

2. ANAXAGOREA ALLENII R. E. Fries, in Ann. Missouri Bot. Gard. 42: 151. 1955.

Tree about 6 m. tall; young branches very shortly rufous-tomentellous. Petiole of leaves 10-12 mm. long, thick; blade chartaceous in desiccation, yellowish green, very glabrous and smooth above, glabrous and paler beneath, oblong-lanceolate, rounded at the base, gradually narrowed toward the tip, 30-35 cm. long and 8-10 cm. broad,

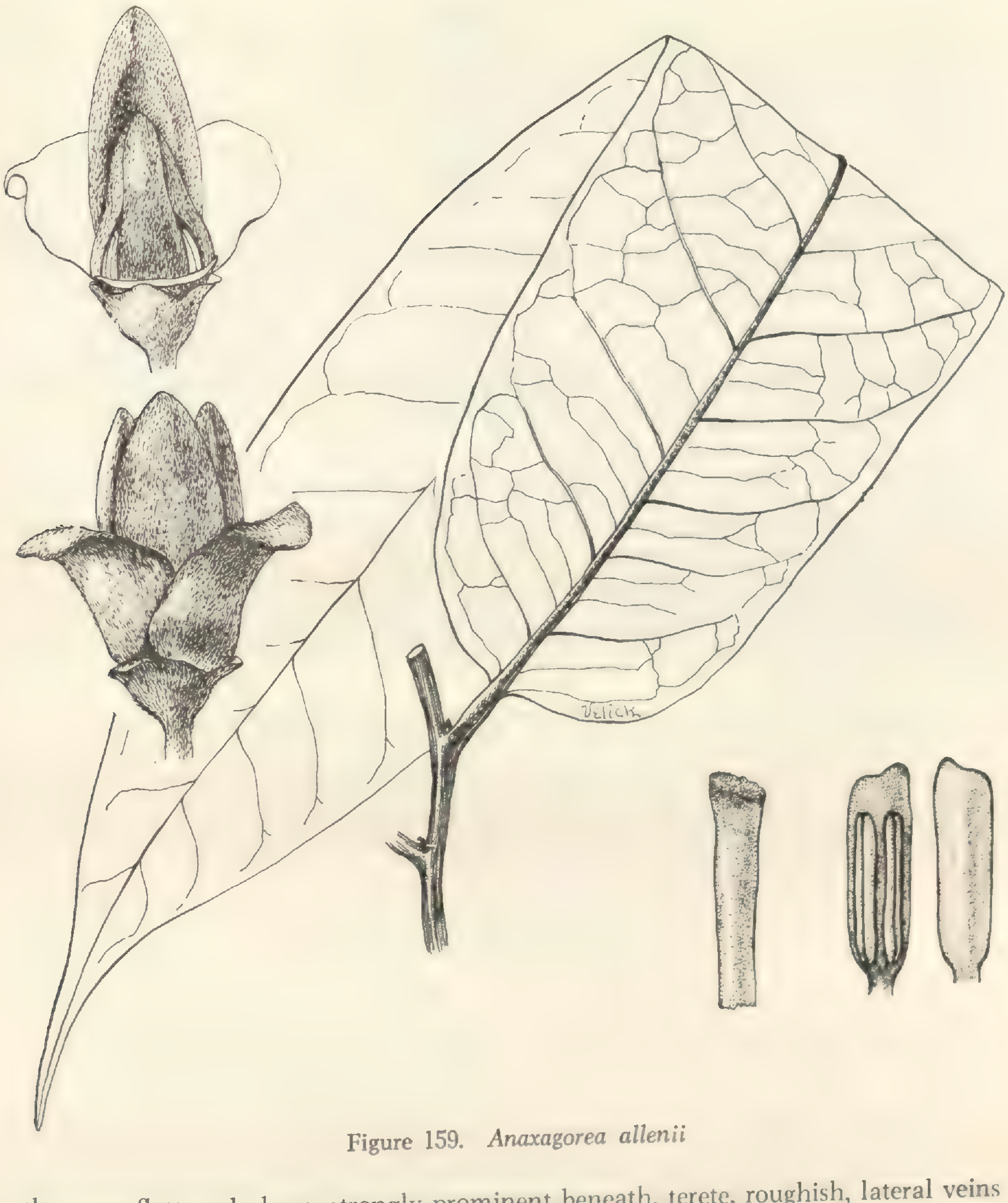

Figure 159. *Anaxagorea allenii*

the costa flattened above, strongly prominent beneath, terete, roughish, lateral veins about 15 on each side, broadly ascending, both the veins and the veinlets somewhat elevated beneath. Pedicels of flowers short, 3-4 mm. long, thick, rufous-tomentellous like the sepals and the petals, provided with a vaginiform bract near the calyx. Sepals ovate-orbicular, rounded at the tip, not recurved, 7-10 mm. long. Petals thick, the outer oblong, rounded and not narrowed toward the tip, but carinate toward the tip within, up to 12 mm. long and 5 mm. broad, the inner lanceolate, very acute, pilose to the middle and carinate above the middle within. Stamens linear, 3 mm. long, the appendage of the connective slender, about 0.7 mm. long, truncate-rounded. Fruit unknown.

CANAL ZONE: Quebrada López, alt. 30 m., *Allen 2143*.

Another species of the genus *Anaxagorea* certainly also occurs in Panamá, as the material available to me from the herbarium of the Missouri Botanical Garden includes a third, collected in the vicinity of the Chiriquí Lagoon (*Von Wedel 2210*). This lacks flowers, however, and it is therefore impossible to determine with any certainty its position in relation to hitherto known species of *Anaxagorea.*

7. DESMOPSIS Saff.

Desmopsis Saff. in Bull. Torrey Bot. Club 43: 184. 1916; R. E. Fries, in Acta Hort. Berg. 10: 16. 1930.

Shrubs or small to medium-sized trees; the pubescence of simple hairs. Flowers medium-sized in few-flowered inflorescences (rhipidia) opposite the leaves or rarely produced from the trunk; pedicels usually long with 2 bracts. Sepals valvate. Petals valvate in bud or a little imbricate at the apex, all rather alike, linear-oblong to lanceolate. Stamens numerous; pollen sacs not locellate; connective expanded above the anther into a truncate disk. Carpels several to numerous with 1-8 lateral ovules. Monocarps stipitate or rarely subsessile, spherical to shortly ovoid-cylindric.

About 13 species, distributed from Mexico down to Panama, one (*neglecta*) endemic on Cuba.

a. Inflorescence peduncle bearing near the apex a foliaceous bract 1-2 cm. long; flower pedicels 2-8 cm. long.
  b. Petals incurved at the tips; monocarps 10-12 cm. across .....1 D. panamensis
  bb. Petals not incurved at the tips; monocarps 6-8 mm. across.
    c. Monocarps with thin stipes 5-8 mm. long.
      d. Leaves acutely acuminate at the apex .....2. D. microcarpa
      dd. Leaves obtuse or rotundate at the apex .....3. D. bibracteata.
    cc. Monocarps with thick stipes 1-3 mm. long .....4. D. maxonii
aa. All bracts very small; flower pedicels about 1 cm. long .....5. D. brevipes.

1. Desmopsis panamensis (Rob.) Saff. in Bull. Torrey Bot. Club 43: 185, *pl.* 7. 1916; R. E. Fries, in Acta Hort. Berg. 10: 18, *fig.* 3, *b.* 1930.

Unona panamensis Rob. in Amer. Journ. Sci. 50: 175. 1895.

Tree 5-8 m. high, young branchlets ferruginous-tomentose. Leaf petioles tomentose, 3-4 mm. long; blades glabrous on the upper side except on the midrib when young, subglabrous underneath with the midrib and thicker nerves tomentellous, elliptic or elliptic-lanceolate, cuneate and acute at the base, obtusely acuminate at the apex, 10-20 cm. long and 4-8 cm. broad. Inflorescences opposite the leaves, 1- to 2-flowered; their peduncle 3-10 mm. long, provided near the apex with a cordate-orbicular, acute, foliaceous bract 1.5-2.0 cm. long; flower pedicel about 7 cm. long, tomentellous, generally curved, bearing below the middle and at the base on the secondary flower small bracts 1-3 mm. long. Sepals triangular, 2-3 mm. long. Petals linear-oblong from a broad base, revolute at the margins and incurved at the apex, 15-25 mm. long. Ovaries 7-15, ovules 2-8. Monocarps shortly cylindric, rounded at both ends, 14-18 mm. long and 10-11 mm. across; stipes 8-10 mm. long.

Figure 160. *Desmopsis microcarpa*

CANAL ZONE: woods near Gatún Station on the old Panamá Railway, *Hayes s.n.*; hills around the Agua Clara Reservoir, near Gatún, alt. 20-30 m., *Pittier 2660.*

Reported also from Barro Colorado Island (Standley, 1933).

2. DESMOPSIS MICROCARPA R. E. Fries, in Acta Hort. Berg. 10: 23. 1930.

Desmopsis glabrata Schery, in Ann. Missouri Bot. Gard. 28: 428. 1941.

Small tree 2-3 m. high, with the young branchlets thinly appressed-hirsute, very soon glabrescent. Leaves on petioles 3-4 mm. long, lanceolate-elliptic to broadly elliptic, rounded to cuneate at the base, rotundate and abruptly acuminate and more or less gradually tapering at the apex, glabrous above except on the more or less hirsute midrib, glabrous beneath, 10-20 cm. long and 4-10 cm. broad. Inflorescences up to 5-flowered; their peduncles about 1 cm. long and bearing near the apex a rotundate-cordate or foliaceous bract 1-2 cm. long; flower pedicels 5-8 cm. long, very slender, provided near the base and below the middle with 2 bracteoles 0.5-1.0 mm. long. Sepals ovate, 3-4 mm. long. Petals narrowly lanceolate, 4-6 mm.

broad at the base, gradually tapering to the blunt apex, sericeous outside, glabrous and black inside. Monocarps 7, spherical or shortly cylindrical, 7-8 mm. across; stipes thin, 6-8 mm. long.

Costa Rica and Panama.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Water Valley, *Von Wedel 1265, 1459, 1565, 1767, 2464;* exact locality lacking, *Von Wedel 279.*

3. DESMOPSIS BIBRACTEATA (Rob.) Saff. in Bull. Torrey Bot. Club. 43: 190, *pl. 9,* 1916.

Unona bibracteata Rob. in Amer. Journ. Sci. 50: 175, 1895.

Shrub or small tree. Leaves on petioles 2-3 mm. long, lustrous on both sides, glabrous above, hirsute beneath at first but soon quite glabrous, oblong-lanceolate or elliptic or rhombic, cuneate at the base, shortly angustate into an obtuse or rotundate apex, 5-14 cm. long, 2.5-5.5 cm. broad. Inflorescences on peduncles 2-5 mm. long, these bearing at the apex a rotundate-cordate, foliaceous bract 0.5-1.5 cm. long; flower solitary; pedicel slender, thinly appressed-hairy, 1.5-2.5 cm. long, provided below the middle with a small foliaceous bract 1-3 mm. long. Petals oblong 10(-18) mm. long and 4-6 mm. broad, sericeous outside. Ovaries 14-20, densely sericeous; ovules 3. Monocarps on stipes about 5 mm. long, subglobose or shortly cylindric, truncate-rotundate or even umbilicate at both ends, constricted between the seeds, 5-10 mm. long and 6-8 mm. broad.

Nicaragua, Costa Rica and Panama.

CHIRIQUÍ: *Pittier 3367, 5747* (according to Safford; the specimens not seen).

4. DESMOPSIS MAXONII Saff. in Bull. Torr. Bot. Club 43: 188, *pl* 8. 1916; R. E. Fries, in Acta Hort. Berg. 10: 24, *fig.* 3, *d-e.* 1930.

Tree 5-7 m. high with appressed-hairy branchlets. Leaves on petioles 5 mm. long, glabrous above, the underside pale fulvous-hirsute at first, finally quite glabrous, broadly elliptic or elliptic-oblong or lanceolate, acute and decurrent at base, acuminate, 10-14 cm. long and 4-8 cm. broad. Inflorescence peduncle 7-14 mm. long, bearing near the apex a suborbicular or broadly ovate, amplexicaul bract, 7-15 mm. broad, flower solitary, pale yellow; its pedicel 3.5-6.0 cm. long, curved, slender and thickened upwards, soon quite glabrous, below the middle bearing a small bracteole. Sepals broadly triangular, 4 mm. long. Petals all uniform, linear-oblong, obtuse, 13-18 mm. long and 4-5 mm. broad, clothed outside with gray appressed minute hairs. Pistils 10-15, ovules 2-5. Monocarps globose or obovoid, about 8 mm. across, subsessile or shortly stipitate, the stipes 1-3 mm. long and 1.5-2.0 mm. thick.

CHIRIQUÍ: in forest near El Boquete, alt. 1000-1300 m., *Pittier 3154;* in the humid forest along the upper Caldera River, above El Boquete, alt. 1450-1650 m., *Maxon 5564.*

5. DESMOPSIS BREVIPES R. E. Fries in Acta Hort. Berg. 13: 107. 1941.

A shrub or tree up to 10 m. tall, the young branchlets ferruginous-strigose, soon glabrescent. Leaf petioles 2-4 mm. long, appressed ferruginous-hirsute on both sides

when young, soon glabrescent, rounded or shortly acute at the base, rather abruptly cuspidate at the apex, 7-15 cm. long, 3-7 cm. broad. Inflorescences with 1-2 (or more ?) flowers opposite the leaves on young branchlets or rarely produced from the trunk; bracts small; pedicels rather thick, ferruginous-sericeous at first, more or less glabrescent, 8-10 mm. long, provided below the middle with a small bract (0.5-1.0 mm. long). Sepals rounded-deltoid, sericeous outside. Petals all uniform, linear-elongate from a dilated base, gradually narrowed into a more or less incurved apex 20-25 mm. long. Ovaries densely sericeous; ovules 3. Monocarps about 12, tomentellous at first, finally glabrescent, black when dried, very shortly stipitate, ellipsoid to more or less spherical, about 1.5 cm. across.

BOCAS DEL TORO: vicinity of Nievecita, *Woodson, Allen & Seibert 1864.*

8. STENANONA Standl.

STENANONA Standl. in Field Mus. Publ. Bot. 8: 205. 1929; R. E. Fries, in Acta Hort. Berg. 10: 151. 1931; 13: 103. 1941.

Small trees. Flowers medium-sized, on short pedicels. Sepals 3, valvate, caudate. Petals 6, biseriate, all similar, long caudate-cuspidate, the outer imbricate and connate with the inner at the base. Stamens numerous; filaments short; anthers oblong, extrorse; pollen sacs not locellate; connective elongated into a deltoid ligule above the anthers. Carpels numerous; ovules 2, lateral.

A small genus of 2 species, 1 of them occurring in Costa Rica, 1 in Panama.—The genus is very little known so far, and more complete material is desirable for a determination of its systematic position.

1. STENANONA PANAMENSIS Standl. in Field Mus. Publ. Bot. 8: 205. 1929.

Tree about 6 m. high; branchlets densely covered with fulvous patent hairs 1.5-2.0 mm. long. Leaves on petioles 2-4 mm. long, membranaceous, sparsely hairy on the upper side, glabrescent, fulvous-hirsute beneath, oblong or obovate-oblong, abruptly acuminate, rotundate or subcordate at the base, 8-18 cm. long and 2.5-6.5 cm. broad. Pedicels hirsute, up to 5 mm. long, bracteate; bract superior, lanceolate, long-acuminate, about 1 cm. long. Sepals ovate, abruptly long-acuminate, 15 mm. long, 5 mm. broad at the base, hirsute on the outside. Petals about 7 cm. long, fleshy, reddish, pilose, 4-5 mm. broad at the base, 0.6 mm. at the apex.

BOCAS DEL TORO: Daytonia Farm, region of Almirante. *Cooper 427.*

9. MALMEA R. E. Fries

MALMEA R. E. Fries, in Arkiv Bot. 5^4: 3. 1905; in Acta Hort. Berg. 10: 37. 1939.

Trees and shrubs. Flowers medium-sized or large, in few- to several-flowered inflorescences opposite the leaves, or rarely pseudo-axillary; pedicels articulated immediately above a nearly basal bract and bearing another bract above the articulation. Sepals small, with thin margins, imbricate in bud. Petals much longer than the sepals, more or less blackening when dried, orbicular-elliptic, imbricate in bud, their margins thin and more or less crispate. Stamens very numerous, the

Figure 161. *Stenanona panamensis*

connective expanded above the anther into a truncate disk; pollen sacs not locellate. Carpels numerous, containing 1 basal, erect ovule. Monocarps free, stipitate, 1-seeded.

Twelve species are known of this genus, 8 inhabiting Ecuador, the Amazonian region and Guiana; 1 is native to Bahia, and 3 are found in Central America (Mexico to Panama). Only 1 species is recorded from Panama.

1. MALMEA HYPOGLAUCA (Standl.) R. E. Fries, in Acta Hort. Berg. 10: 321. 1931.
Guatteria hypoglauca Standl. in Field Mus. Publ. Bot. 4: 207. 1929.

A tree up to 10 m. high; young branchlets glabrous. Leaves on petioles 5-6 mm. long, glabrous and glaucous beneath, elliptic or oblong-elliptic, rounded at the base and shortly decurrent, shortly acuminate at the obtuse apex, 12-14 cm. long and 5-6 cm. broad. Inflorescences terminal (or opposite the leaves ?); pedicels about 5 mm. long, thinly ferruginous-hirsute. Sepals 2-3 mm. long. Petals thick and glabrous, blackening when dried, elliptic-obovate and rotundate at the apex, 15-18 mm. long and 11-12 mm. broad. Stamens 2 mm. long. Fruit unknown.

SAN BLAS: Permé, *Cooper 661*.

This species is also found in Colombia (Department of Antioquía).

10. PORCELIA R. & P.

PORCELIA R. & P., Fl. Peruv. & Chil. Prodr. 84, *tab. 16*. 1794; R. E. Fries, in Acta Hort. Berg. 10: 28, *fig. 4*. 1930.

Trees. Leaves ovate to lanceolate-oblong, nearly glabrous, with translucent glands. Flowers medium-sized, bisexual or polygamous, terminal or opposite the leaves, often produced on axillary, very reduced branchlets (pseudo-axillary flowers); pedicels articulate at the base, without bracts. Sepals small. Petals imbricate in bud and finally widely spreading, all of about the same size, oblong-ovate or obovate. Stamens numerous; pollen sacs locellate; connective expanded above the anther into a truncate disk. Ovules numerous, lateral. Monocarps (sometimes very) large, free, stipitate, ellipsoid-cylindric, with large, reniform seeds.

A small genus of 5 species. Two of them (*macrocarpa* and *goyazensis*) are indigenous in eastern Brazil, 1 (*nitidifolia*) in Peru and Ecuador, 1 (*steinbachii*) in eastern Bolivia and adjacent parts of the Amazonas basin and 1 (*magnifructa*) in Panama and Venezuela.

1. PORCELIA MAGNIFRUCTA (Schery) R. E. Fries, in Arkiv Bot. andra ser. 1: 343. 1950.
Cymbopetalum magnifructum Schery, in Ann. Missouri Bot. Gard. 30: 87. 1943.

A tree about 12 m. high; young shoots and pedicels densely tomentellous, ochraceous, finally glabrous. Leaves on petioles 2-8 mm. long, ovate to oblong, rotundate to shortly acute at the base, longer acuminate at the apex, grey-ochraceous

Figure 162. *Porcelia magnifructa*

tomentellous at first on both sides, especially beneath, soon glabrescent with translucent glands, up to 15 cm. long and 4-5 cm. broad. Pedicels 2-3 cm. long, without bracts. Sepals ovate, 3-5 mm. long, grey-tomentellous. Petals ovate, the apex rotundate and more or less incurved when dried, up to 17 mm. long, tomentellous on both sides. Stamens 2.5-3.0 mm. long, pollen sacs locellate. Carpels 10-15. Monocarps large, 6-10 cm. long and about 6 cm. across, ovoid; pericarp thick, ligneous. Seeds 2.5-3.0 cm. long.

PANAMÁ: vicinity of Bejuco, alt. ca. 50 m., *Allen 2455*.—Apparently also in Venezuela.

11. CYMBOPETALUM Benth.

CYMBOPETALUM Benth. in Journ. Linn. Soc. 5: 69. 1861; R. E. Fries, in Acta Hort. Berg. 10: 180. 1931.

Trees or shrubs with large, rather thin leaves. Flowers solitary, usually produced from the internode above the axil, sometimes terminal or rarely pseudo-axillary; pedicels often long, articulate at the base, without bracts. Perianth segments valvate in bud; sepals small; outer petals flat and thin, the inner longer, thick and fleshy with involute margins, cymbiform. Stamens numerous; pollen sacs

locellate; connective expanded above the anther into a truncate disk. Fruit of several free, oblong-cylindric monocarps, containing several (4-14) lateral seeds.

A small genus of 19 species, distributed from Mexico to Brazil (Rio de Janeiro). Only 3 species are found in Panama.

a. Pedicels 5 cm. long or generally much longer; flowers large; inner petals 2.5-3.5 cm long; stamens 4.0-4.5 mm. long.
   b. Leaves obovate-oblanceolate, long-cuneate at the base. .....1. C. BRASILIENSE.
   bb. Leaves narrowly oblong-lanceolate, rounded-acute at the base. 2. C. LANUGIPETALUM.
aa. Pedicels about 3 cm. long; flowers small; inner petals 1.5 cm. long; stamens 2.0-2.5 mm. long .....3. C. COSTARICENSE.

1. CYMBOPETALUM BRASILIENSE (Vell.) Benth. in Journ. Linn. Soc. 5: 69. 1861; R. E. Fries, in Svensk. Vet.-Akad. Handl. ser. 3. 24[10]: 29. 1900.

Uvaria brasiliensis Vell. Fl. Flumin. 238. 1825; 5: *tab. 122.* 1827; Eichl. in Mart. Fl. Bras. 13[1]: 39, *tab. 13, fig. 2.* 1841.

Unona viridiflora Splitg. in Nederl. Kruidk. Arch. 1: 224. 1848.

Uvaria viridiflora Walp. Ann. Bot. Syst. 2: 19. 1851.

Eschweilera simplex Miers, in Trans. Linn. Soc. 30: 264. 1875.

Trigynaeia anastomosans Rusby, Descr. New Species of S. Amer. Plants 19. 1920.

Uva brasiliensis O. Ktze. Rev. Gen. 7. 1891.

A small tree with shortly puberulous branchlets, soon glabrescent. Leaves on petioles 3-4 mm. long, membranaceous, glabrous and densely pellucid-punctate, obovate, oblanceolate, or lanceolate-elliptic, cuneate-angustate toward the base, 15-30 cm. long and 6-10 cm. broad. Pedicels 5-9 cm. long, glabrous. Sepals connate at the base, rounded-reniform, obtusely acuminate, 4-6 mm. long and 6-9 mm. broad. Petals tomentellous on both sides, the outer ovate or rotundate, flat, 2.0-2.5 cm. long and 2-3 cm. broad, the inner thick, rounded-elliptic, obtuse, 2.5 -3.5 cm. long and 1.8-2.3 cm. broad, the margins involute. Stamens 4.0-4.5 mm. long. Monocarps numerous, oblong-cylindric, and more or less curved, torulose, rounded at both ends, up to 3.5 cm. long and 1.5 cm. broad. Seeds up to 6, but generally fewer.

This species is distributed in eastern South America from Trinidad and Venezuela down to Rio de Janeiro; in western South America from Panama to south Colombia.

DARIÉN: Río Cuasi, alt. 800 ft., *Terry & Terry 1417.*

2. CYMBOPETALUM LANUGIPETALUM Woods. & Schery, in Ann. Missouri Bot. Gard. 28: 427. 1941.

Tree; young branchlets very shortly appressed-hirsute. Leaves on very short petioles (1-2 mm. long), rigid, glabrous on both sides, oblong-lanceolate, rounded or very shortly acute at the base, gradually tapering toward a long narrow cusp, 15-30 cm. long and 5-7 cm. broad, the nerves impressed on the upper side, very prominent beneath. Flowers solitary; pedicels glabrous, pendulous, about 20 cm.

Figure 163. *Cymbopetalum lanugipetalum*

long. Sepals small, about 0.3 cm. long. Outer petals flat and thin, subtriangular, 1.8-2.0 cm. long and 1.0-1.6 cm. broad, the inner fleshy and tomentellous, triangular-ovate, cymbiform, about 3 cm. long and 1.5 cm. broad. Stamens 4-5 mm. long, the pollen sacs locellate, the connective-appendage globose, setulose.

COCLÉ: north rim of El Valle de Antón near Cerro Turega, alt. 650-700 m., *Woodson & Schery 191a.*

3. CYMBOPETALUM COSTARICENSE (Donn. Sm.) R. E. Fries, in Acta Hort. Berg. 10: 186, *fig. 6 a-c d.* 1931.

Asimina costaricensis Donn. Sm. in Bot. Gaz. 23: 2. 1897.

Tree or shrub; young branchlets sparsely clothed with very short appressed hairs, soon glabrescent and densely provided with lenticels. Leaves on petioles 4-6 mm. long, membranaceous, finally glabrous, verruculose along the thicker nerves, oblong, elliptic-oblong or obovate, cuneate at the base, rather abruptly cuspidate, 10-22 cm. long, 4.0-6.5 cm. broad. Pedicels about 3 cm. long. Sepals rounded-ovate, shortly apiculate, about 4 mm. long. Petals grey-tomentellous, the outer flat, broadly ovate, acute, up to 12-13 mm. long, the inner obovate-rotundate, about 17 mm. long and 10 mm. broad, narrowed at the base into a petiole 5 mm. long, the margins of the upper part striate and involute. Stamens 2.5 mm. long, connective-disk plane and tomentellous. Monocarps 8-10, shortly cylindric, not torulose, 3-5 cm. long and about 1.7 cm. thick. Seeds 12-14.

Costa Rica and Panama.

BOCAS DEL TORO: Daytonia Farm, *Cooper 624;* vicinity of Chiriquí Lagoon, Water Valley, *Von Wedel 693, 1768.*

12. DUGUETIA St. Hil.

DUGUETIA St. Hil. Fl. Bras. Mer. 1: 35, *t.* 7. 1825; R. E. Fries, in Acta Hort. Berg. 12: 28. 1934.

Trees or shrubs with stellate hairs or stellate scales. Flowers medium-sized or large in few- or multi-flowered inflorescences; these more or less strictly opposite the leaves, or sometimes produced from older branches or from the trunk. Sepals valvate. Petals free, generally imbricate in bud. Stamens numerous; connective generally expanded above the anther into a truncate disk. Carpels numerous; ovules solitary, basal, erect. Monocarps sessile, closely crowded, ligneous or fleshy, easily separable or more or less coherent.

A large genus (about 70 species), distributed from Panama and the West Indies to southern Brazil and Paraguay; especially rich in the Amazonian region and Guiana.

a. Stellate scales abundant; monocarps very rugose above the middle .....1. D. PANAMENSIS.
aa. No scales, only stellate hairs; monocarps smooth .....2. D. VALLICOLA.

1. DUGUETIA PANAMENSIS Standl. in Field Mus. Publ. Bot. 4: 207. 1929; R. E. Fries, in Acta Hort. Berg. 12: 53. 1934.

A tree about 10 m. high, the young branchlets densely covered with golden-yellow stellate scales. Leaves on 3-4 mm. long petioles, 12-22 cm. long and 3.5-5.0 cm. broad, chartaceous, glabrous on upper side from the first, densely scaly underneath when young, finally nearly glabrescent, oblanceolate, cuneate and very acute at the base, contracted at the apex into an obtuse acumen 1.5-3.0 cm. long. Inflorescences 1- to 3-flowered, opposite the leaves, shortly pedunculate. Flowers on pedicels 2-4 mm. long, small, fragrant. Sepals about 10 mm. long, ovate, yellow-

scaly outside. Petals oblong, obtuse, rather densely silvery-scaly outside, up to 13 mm. long and 5 mm. broad. Stamens 1 mm. long, the connective-disk glabrous. Ovaries glabrous. Fruit spherical, 3.5-4.5 cm. across; monocarps numerous, free, clavate, 16-18 mm. long and 7-8 mm. thick, very rugose above the middle, rotundate and very shortly apiculate at the apex.

BOCAS DEL TORO: region of Almirante, Daytonia Farm, Jan. 1928, *Cooper 418*.

The appearance of the fruit of this species is unique in its genus. Towards their upper parts, the monocarps are densely covered by protuberant, conical, and acuminate excrescences, about a millimetre long, making their appearance so foreign to the genus that the specimen might easily be taken for a monstrosity (galls ?). Nevertheless, the species is well differentiated from the other Duguetias also by other characters.

2. DUGUETIA VALLICOLA Macbr. in Contr. Gray Herb. n. ser. 56: 51. 1918; R. E. Fries, in Acta Hort. Berg. 12: 85. 1934.

A shrub or tree, up to 20-25 m. high. Leaves on petioles 4-7 mm. long, provided at first with small stellate grayish hairs on the upper side and finally glabrescent, densely stellate-hirsute at first beneath, finally nearly glabrous with scattered hairs, oblong-lanceolate or narrowly elliptic, rather gradually tapering at the apex, narrowed into the rotundate-obtuse or shortly acute base, 15-30 cm. long and 4.5-8.0 cm. broad. Flowers opposite the leaves or below the nodes; pedicels gray-tomentellous, 12-15 mm. long (in fruits up to 25 mm.). Sepals reflexed, ovate, gray-tomentellous on both sides, 8-12 mm. long. Petals ovate, obtuse, longitudinally striate at the base, densely covered on both sides with very short, gray, stellate hairs, up to 2.5 cm. long and 1.5 cm. broad. Stamens 1.3-1.5 mm. long. Fruit 4.0-4.5 cm. diam.; monocarps free, glabrous but more or less pruinose, obovoid, pentagonal, shortly apiculate, up to 18 mm. long and 7-8 mm. across.

DARIÉN: forest around Pinogana, *Pittier 6565*.

Described from Colombia, Magdalena Valley; probably also occurring in Venezuela.

13. ANNONA L.

ANNONA L. Sp. Pl. 536. 1753 *[Anona]*.

Shrubs or trees with simple or stellate hairs. Flowers solitary or in few-flowered inflorescences, terminal or opposite the leaves, or extra-axillary from the internodes. Sepals 3, small, valvate. Petals 6, free or connate at the base, biseriate, or the inner rudimentary or absent, the outer valvate, the inner imbricate or valvate. Stamens numerous, the anther cells not locellate, the connective generally terminating in a swollen head or hoodlike process above the pollen sacs. Carpels numerous or rarely few; ovule 1, basal, erect. Fruit fleshy, formed by the concrescence of the carpels and the torus, usually areolate on the surface, the areoles, indicating the united carpels, being often gibbous or acuminate.

Figure 164. *Duguetia panamensis*

A large genus of about 110 species in all the tropics of America from Florida, Mexico and the West Indies to southern Brazil and Paraguay. A few species also in tropical Africa. Five indigenous species are recorded from Panama.

a. Petals 6.
  b. Petals free.
    c. Branchlets and leaves glabrous; sepals 3-5 mm. long; petals about 3 mm. long, the inner valvate ..... 1. A. GLABRA.
    cc. Branchlets and leaves hirsute; sepals 1-2 cm. long; outer petals up to 5 cm. long, the inner imbricate ..... 2. A PURPUREA.
  bb. Petals connate at base ..... 5. A. HAYESII
aa. Petals 3, the inner missing or very rudimentary.
  b. Leaves thickly tomentose beneath, 10-20 cm. long ..... 3. A. SPRAGUEI.
  bb. Leaves glabrous, 6-8 cm. long ..... 4. A. ACUMINATA.

1. ANNONA GLABRA L. Sp. Pl. 537. 1753.

Anona palustris L. Sp. Pl. 757. 1762.

Anona laurifolia Dunal, Monogr. Anonac. 65. 1817.

Anona peruviana Humb. & Bonpl. ex Dunal, l. c. 67. 1817.

Anona uliginosa H. B. K. Nov. Gen. & Sp. Pl. 5: 65. 1821.

Anona australis St. Hil. Fl. Bras. Mer. 1: 33. 1825.

Anona pisonis St. Hil. & Tul. in Ann. Sci. Nat. sér. 2. 17: 131. 1842, non Mart.

A tree up to 10 metres high; branchlets very soon glabrous. Leaves on petioles 1.0-1.5(-2.5) cm. long, rather thin, pale green, ovate-elliptic or oblong-elliptic, rotundate or acute and decurrent at the base, shortly acute or rarely obtuse at the apex, 7-14 cm. long and 3-8 cm. broad; network of veins dense and nicely prominent on both sides. Flowers solitary, issuing from about the middle of the internodes below the leaves; pedicels 1.5-2.0 cm. long, glabrous. Sepals rotundate, apiculate, 3-5 mm. long. Petals glabrous on outside, the outer ovate, 2.5-3.0(-4.0) cm. long, the inner a little smaller. Stamens 3-4 mm. long, connective disk broad, papillose but not setose. Fruit globose-ovoid, rounded at the top, 7-12 cm. long, smooth, areoles hardly obvious.

This species is distributed from Mexico and the West Indies southwards to Ecuador on the west side and to southern Brazil on the east, also on the west coast of tropical Africa; always growing near the sea in littoral forests, in mangrove swamps and on riverbanks.

CANAL ZONE: Chagres, *Fendler 1;* forest at Río Indio de Gatún, near sea-level, *Pittier 2809;* in swampy places near Panamá, *S. Hayes s.n.* BOCAS DEL TORO: Old Bank Island, *Von Wedel 2082.*

Also reported from Barro Colorado Island (Standley, 1933).

2. ANNONA PURPUREA Moc. & Sesse, ex Dunal, Monogr. Anonac. 64, *tab.* 2. 1817.

Anona manirote H. B. K. Nov. Gen. & Sp. Pl. 5: 59. 1821.

Anona involucrata Baill. in Adansonia 8: 265. 1867-68.

Anona prestoei Hemsl. in Hook. Ic. Pl. 4: 6, *t.* 2519-20. 1897.

Tree with ferruginous-tomentose branchlets. Leaves deciduous, on 3-5 mm. long petioles, membranaceous, on the upper side shortly and thinly, on the nerves more densely hirsute, finally more or less glabrate, underneath longer ferruginous-hirsute along the nerves, obovate or elliptic-obovate, rotundate at the base, shortly acuminate at the apex, 12-30 cm. long and 6-14 cm. broad. Flowers solitary, subsessile; flower bud enclosed at first by an involucre composed of 2 sessile acuminate bracts. Calyx lobes triangular-ovate, acuminate, 1-2 cm. long. Outer petals valvate, thick, rigid, ovate-lanceolate, gradually tapering into a long, obtuse apex, up to 5 cm. long and 2 cm. broad, ferruginous-sericeous on the outside, inner petals imbricate, thinner, elliptic-oblong, rotundate at the apex, 2.5 cm. long. Stamens 5-6 mm. long. Fruit globose, up to 20 cm. in diameter, bearing numerous pyramidal protuberances and clothed with brown felt-like tomentum. Seeds 28-30 cm. long.

This species is recorded from Mexico, British Honduras, Costa Rica, Panama, Venezuela, Ecuador and Trinidad.

CANAL ZONE: Ancón Hill, alt. 200 ft. *Allen 4521;* Hospital grounds, Ancón, *Pittier* 3955; Barro Colorado Island, *Bangham 610;* Matachín, on Panamá Railway, *Hayes s.n.* CHIRIQUÍ: forest of San Félix, *Pittier, 5749;* Chiriquí, *Cooper & Slater P 314.*

The species "is common on the Pacific slope" (Standley, 1928, p. 180).

3. ANNONA SPRAGUEI Saff. in Contr. U. S. Nat. Herb. 16: 270, *fig.* 43, *pl.* 92-93 1913.

Anona uncinata Sprague, in Bull. Herb. Boiss. sér. 2. 5: 701. 1905, non Lam.

A tree up to 16 m. high; young branchlets ferruginous-tomentose, soon glabrescent. Leaves on petioles 8-15 mm. long, membranaceous, pellucid-punctulate, sparsely pubescent above, at first very densely and softly sericeous-pubescent beneath with appressed grayish olivaceous hairs, rufous-tomentose along the midrib and lateral nerves, lanceolate to oblanceolate or narrowly elliptic, shortly acute or sometimes subrotundate at the base, acuminate at the apex, 15-35 cm. long and 5-11 cm. broad. Flowers solitary; pedicels about 1 cm. long, in fruit up to 2 cm. long (or longer ?); flower buds globose. Sepals long-caudate from an ovate base, 8-10 mm. long. Petals thick, rotundate-ovate, 18-25 mm. long, tomentellous on the outside. Stamens 3.0-3.5 mm. long. Fruit globose or globose-ovoid, about 5 cm. in diameter; the areoles produced into long-attenuate protuberances. Seeds oblong, 7-9 mm. long.

Known only from Panamá.

CANAL ZONE: Gamboa, *Pittier* 3409; R. Cocoli, opposite lighthouse, *P. White 99;* Frijoles, *Standley 27570.* PANAMÁ: San José Island, Perlas Archipelago, *Johnston* 734; Barbacoas, *Hayes 127;* Tapía River, Juan Díaz region, *Maxon & Harvey* 6649. DARIÉN: Marraganti and vicinity, Río Tuyra, 10-200 ft. elev., *Williams;* forest around Yaviza, *Pittier* 6540.

Also reported from Barro Colorado Island (Standley 1933).

4. ANNONA ACUMINATA Staff. in Contr. U. S. Nat. Herb. 16: 274. *pl.* 97. 1913.

Anona echinata Hemsl. Biol. Centr.-Amer. Bot. 1: 19. 1879, non Dunal.

Tree, 5-7 m. high; young branchlets clothed with very minute appressed hairs, soon glabrate. Leaves on petioles 3-5 mm. long, membranaceous, finally glabrous, pellucid-punctulate, lanceolate or oblong-elliptical, acute and decurrent at the base

Figure 165. *Annona acuminata*

and gradually acuminate at the apex, 5-9 cm. long and 1.5-2.5 cm. broad. Flowers solitary, more or less opposite the leaves; pedicels 12-16 mm. long, with 2 linear-lanceolate bracts 2-4 mm. long; flower buds subglobose, about 15 mm. in diameter. Sepals high-connate, appressed-pilose on the outside. Petals 3, ovate-rotundate, connate at the base, 12-15 mm. long and broad. Stamens 2.5 mm. long; connective disk muriculate with short stiff points. Fruit globose, 2.0-2.5 cm. in diameter, with conical spines 1 mm. long. Seeds yellow, 7-8 mm. long.

Recorded only from Panamá.

CANAL ZONE: vicinity of Salamanca Hydrographic Station, Río Pequení, alt. ca. 80 m., *Woodson, Allen & Seibert 1564;* drowned forest of Quebrada Tranquilla and its branches, *Dodge & Allen 17331;* Bohío station, Panamá railroad, *Hayes 142.* PANAMÁ: Río Tapía, *Standley 26212, 28036.*

Reported from Barro Colorado Island (Standley 1933).

5. ANNONA HAYESII Saff. ex Standley, in Journ. Washington Acad. Sci. 15: 102. 1925; R. E. Fries, in Acta Hort. Berg. 10: 273, *tab. 21.* 1931.

A high shrub or small tree; branchlets densely sericeous-tomentose, ferruginous. Leaves on petioles 3-7 mm. long, thin-membranaceous, underneath pale and at first appressed-hirsute, soon glabrous except on the nerves, obovate or elliptic, abruptly acuminate and rather rotundate at the base, 8-12(-25) cm. long and 4-9 cm. broad. Inflorescences opposite the leaves or produced from the middle of the internodes below the leaves, 1- or few-flowered; pedicels 12-15 mm. long, densely ferruginous-hirsute; flower buds long-caudate from a globose base. Sepals ovate, acuminate. Outer petals up to 30 mm, long, connate up to 5 mm. above the base, the base ovate, abruptly narrowed into a linear obtuse acumen nearly 20 mm. long, rufous sericeous-tomentellous on the outside; inner petals minute, 5-7 mm. long, connate with the outer at the base. Stamens 1.2-15 mm. long, the connective disk narrower than the anther. Fruit subglobose, smooth, 5 cm. long or more.

Found only in Panama.

CANAL ZONE: Ancón Hill, alt. 200 ft., *Allen 4521;* Corozal, *Gervais 141.* DARIÉN: forest at Yaviza, *Pittier 6592;* La Palma, alt. 50 m., *Pittier 6598.* PANAMÁ: thickets and forests near Arraiján, alt. ca. 15 m., *Woodson, Allen & Seibert 1372;* Matías Hernández, *Pittier 6749.*

Also reported from Barro Colorado Island (Standley, 1933).

14. ROLLINIA St. Hil.

ROLLINIA St. Hil. Fl. Bras. Merid. 1: 28, *t.* 5. 1825; R. E. Fries, in Acta Hort. Berg. 12: 112. 1934.

Trees and shrubs. Flowers usually clustered in inflorescences opposite the leaves, or extra-axillary from the internodes. Sepals small, valvate. Petals valvate, connate at the base, the outer produced on their outside into a wing or spur. Stamens numerous, their anther cells not locellate; connective expanded above the anther into a truncate disk. Carpels several to numerous, united into a fleshy syncarpium; ovule solitary, basal, erect.

A large genus of about 62 species, distrubuted from Central America and the West Indies to southern Brazil, Paraguay and northern Argentina. Only 3 species are recorded from Panama.

a. Sepals thin, flat, not keeled; petal wings spreading and curved upward a little ..... 1. R. PERMENSIS.

aa. Sepals more or less concave, the midrib thickened and keeled on the outside.

b. Sepals about 3 mm. long; petal wings recurved ..... 2. R. PITTIERI

bb. Sepals very small, 1.0-1.5 mm. long; petal wings spreading but not recurved ..... 3. R. MICROSEPALA

Rollinia chocoënsis R. E. Fr., which, according to E. P. Killip, occurs "along the Pacific coast of Colombia from the Darién region of Panama into northern Ecuador" (cf. R. E. Fries in Sv. Vet.-Akad. Handl., ser. 3, 24[10]: 18. 1948), might possibly be added to the above. As, however, no specimen from Panama has been available and as it is hard to distinguish it from closely related species, it is perhaps better for the time being not to include it in the flora of that country.

1. Rollinia permensis Standl. in Field Mus. Publ. Bot 4: 208. 1929.

A small tree about 6 m. high; young branchlets, petioles and flower-pedicels covered with ferruginous appressed to patent hairs. Leaves membranaceous, 20-30 cm. long and 8-13 cm. broad, obovate or elliptic-obovate, cuneate or shortly rotundate-acute at the base, 2-3 cm. long, cuspidate at the apex; upper side thinly hairy when young, soon glabrescent, with persistent hairs on the impressed midrib and thicker nerves, densely hairy underneath, finally nearly glabrescent, the midrib with short appressed glossy hairs. Inflorescences more or less opposite the leaves on peduncles about 3 mm. long, bearing up to 8 flowers; pedicels up to 2.5 cm. long. Sepals rotundate-ovate, ferruginous-sericeous, 3-4 mm. long. Corolla 2.0-2.5 cm. across, tomentellous, gray at the base, more densely ferruginous upward; wings divergent and curved upwards a little, oblong, about 10 mm. long and 5 mm. broad.

chiriquí: *Cooper & Slater 211*. san blas: Permé, *Cooper 645*.

2. Rollinia pittieri Saff. in Journ. Washington Acad. Sci. 6: 376. 1916.

Tree with the young branchlets very shortly sericeous. Leaves on petioles 7-12 mm. long, membranaceous, 8-20 cm. long and 4.5-8.5 cm. broad, elliptic or obovate-elliptic, shortly rotundate-acute at the base, abruptly contracted at the apex into a cusp about 1 cm. long, nearly glabrescent above, glaucous beneath, the nerves cinnamomeous and rather densely covered with short appressed white hairs. Inflorescences sessile, opposite the leaves or issuing a little below the nodes; flowers up to 6, on pedicels 3.5(-5.0) cm. long. Sepals triangular, 2-3 mm. long, the midrib thickened and keeled on the outside. Corolla 2.5-3.0 cm. across; wings very densely and shortly silvery-tomentellous, obviously recurved, 1.0-1.5 cm. long and 0.7-1.0 cm. broad. (Fruits unknown).

san blas: plain of Sperdi, near Puerto Obaldía, near sea level, *Pittier 4358*.

3. Rollinia microsepala Standl. in Field. Mus. Publ. Bot. 4: 208. 1929.

Young branchlets fulvous-sericeous, the hairs short-appressed. Leaves on petioles 6-10 mm. long, 10-18 cm. long and 3.5-5.0 cm. broad, oblong or lanceolate-oblong, gradually narrowed at the apex, acute or rotundate at the base, glabrous above and shortly sericeous beneath. Inflorescences about 3-flowered, opposite the leaves or produced a little below the nodes; pedicels densely sericeous, 15-18 mm. long. Sepals minute (1.3-1.8 mm. long), curvate, concave, sericeous. Corolla gray, tomentellous; petal wings cuneate or narrowly obovate, broadly rotundate at the

apex, spreading but not recurved, 15-18 mm. long and 8-10 mm. broad. Stamens 0.6 mm. long. Fruit globose, rather smooth and very shortly tomentellous, 15-17 mm. diam.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 9, 102.*
This species is also recorded from Costa Rica: San Carlos, *Kotschny.*

Figure 166. *Rollinia permensis*

MYRISTICACEAE

By J. A. DUKE

Aromatic trees or shrubs, not infrequently with buttressed bases, whorled branches, stellate pubescence, and reddish sap. Leaves alternate, exstipulate, penninerved, entire, often coriaceous, occasionally with pellucid punctation or stellate pubescence. Flowers unisexual, usually dioecious, actinomorphic, basically trimerous, solitary or more usually fascicled in racemes or panicles, or in dichotomous cymes. Perianth uniseriate, of typically 3 partially fused carnose tepals. Stamens 2-30, the filaments united into a column, the 2-locular extrorse anthers free or coherent to the column. Pistillodes absent. Ovary superior, 1-carpellate, the stigma subsessile; with a single basal anatropous ovule. Fruit fleshy, the thick pericarp splitting longitudinally into 2 valves, the seed often with a reddish laciniate aril, the endosperm ruminate.

A tropical group of about 15 genera centered in America, Africa and Asia, this family is represented in the Americas by 6 genera, 1 of them including the nutmeg of commerce *Myristica fragrans*, locally introduced. Little can be added to the excellent monograph of the American representatives by A. C. Smith (in Brittonia 2: 393. 1937). Four of the 6 American genera occur in Panama.

a. Leaves and young twigs glabrous; secondary veins 4-12 pairs, the tertiary veins sometimes conspicuously parallel, almost perpendicular to the midrib; anthers 4-30, at least as long as the column.

b. Tertiary veins not conspicuously perpendicular to the midrib; staminate flowers few in dichotomously branching cymes, the perianth 3-7 mm. long; anthers 12-30; pistillate pedicels 6-20 mm. long; arils laciniate .....1. Myristica

bb. Tertiary veins strikingly perpendicular to the midrib; staminate flowers several, fasciculate in subspicate racemes, the perianth 1.5-3.0 mm. long; anthers 4-8; pistillate pedicels 2-4 mm. long; arils subentire .....2. Compsoneura

aa. Leaves and young twigs pubescent, occasionally glabrate; secondary veins 5-35 pairs, the tertiary veins not conspicuously perpendicular to the midrib; anthers 3 (-2-6), longer or shorter than the column.

c. Hairs of the young branchlets and petioles with only 1 or 2 conspicuous branches; secondary veins 5-25 pairs; staminate fascicles subcorymbosely to spicately disposed, the anthers usually free to their bases, rarely connate dorsally .....3. Dialyanthera

cc. Hairs of the young branchlets and petioles with several conspicuous branches; secondary veins 10-35 pairs; staminate fasicles racemosely or paniculately disposed, the anthers dorsally connate or distally divergent, never free to their bases .....4. Virola

1. MYRISTICA Boehm.

Myristica [L.]Boehm. in Ludw. Def. 3: 513. 1760, nom. conserv.

Comacum Adans. Fam. 2: 345. 1763, nom. rejic.

Aromatic, glabrous, dioecious trees, the bases occasionally buttressed. Leaves alternate, subdistichous, glabrous, subcoriaceous, petiolate, exstipulate, the tertiary veins obscure. Flowers rather large for the family, the bracteate pedicels glabrous.

Staminate flowers 1-20 in dichotomously branching cymes; tepals partially connate, usually 3, the anthers 12-30, usually longer than the column. Pistillate flowers commonly solitary, the tepals partly connate, the 1-carpellate ovary with a subsessile 2-lobed stigma. Fruits fleshy, the thick pericarp dehiscing longitudinally into 2 valves; aril usually brightly colored and laciniate; seed ellipsoid to globose.

Of this austral Asian genus of around 75 species, only the commonly cultivated nutmeg, a native of the Moluccas, is found in Panama.

Figure 167. *Myristica fragrans*

1. MYRISTICA FRAGRANS Houtt. Handleid. Hist. Nat. Linn. 2: 333. 1774.
Myristica officinalis L.f. Suppl. 262. 1781.
Myristica moschata Thunb. in Vet. Akad. Handl. Stockh. 49. 1782.
Myristica aromatica Lam. Act. Acad. Sci. Paris 1788: 155. 1791.

Aromatic, dioecious, glabrate trees to 20 m. high, the older bark rather smooth and olivaceous, mottled with white, the younger branches often mottled with red. Leaves subcoriaceous, glabrous, lanceolate to ovate or obovate, apically acute to acuminate, basally acute, 6-12 cm. long, 3-6 cm. broad, with usually 6-11 pairs of secondary veins, the tertiary nerves obscure, not conspicuously perpendicular to the midrib, the petioles 5-15 mm. long, ca. 1 mm. broad. Staminate flowers 1 to few in dichotomous cymes; pedicels glabrous, 5-15 mm. long; bracts ca. 1 mm. long; perianth tardily 3-parted, 3-7 mm. long; anthers 12-30, 2-3 mm. long, dorsally coherent to the column, the infra-antheral portion of the column 1-2 mm. long. Pistillate flowers solitary or rarely paired in the axils; pedicels glabrous, 5-15 mm. long; bracts ca. 1 mm. long; perianth accrescent, tardily 3-parted, the segments deltoid, the subsessile stigma obscurely 2-lobed. Fruit fleshy, ovoid to pyriform, the pericarp splitting longitudinally into 2 valves, 3-6 cm. long, 2.5-4.5 cm. broad; seed 1.5-4.5 cm. long, 1.0-2.5 cm. broad, the laciniate aril reddish.

Native to the Moluccas, widely cultivated in tropical America.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *Von Wedel 1232.*

Many spices are extracted from this utilitarian tree, now largely cultivated in southeastern Asia and Grenada. Mace is derived from the aril, and nutmeg from the pulverized seed; a non-drying oil, the so-called nutmeg butter, is also expressed from the seeds. Rumor has it that imperial bureaucrats of little botanic bent once ordered a speedup in the culture of nutmeg trees and a cutback in production for mace trees.

2. COMPSONEURA Warb.

Figure 168. *Compsoneura sprucei*

Compsoneura Warb. in Ber. Deutsch. Bot. Ges. 13: 83, 1895, hyponym; in Nov. Act. Acad. Leop.-Carol. 68: 125. 1897.

Dioecious glabrous shrubs or trees, the sap often reddish. Leaves alternate, glabrous, chartaceous to coriaceous, petiolate, exstipulate, the tertiary veins parallel, conspicuously perpendicular to the midrib. Flower fascicles in spikes, racemes or panicles, the axes glabrous, the bracts absent or inconspicuous. Staminate flowers 3-25 per fascicle, the 3 (-5) tepals partially united; anthers 4-10, as long as or longer than the column. Pistillate flowers 1-8 per fascicle, the tepals partly connate, the 1-carpellate ovary with a subsessile 2-lobed stigma. Fruits fleshy, the thin pericarp dehiscing longitudinally into 2 valves; aril usually brightly colored and subentire; seed ellipsoid.

In this genus of 8 species, that which occurs in Panama essentially covers the entire range of the genus, from southern Mexico through Central America to Amazonian Peru and Brazil.

1. COMPSONEURA SPRUCEI (A. DC.) Warb. in Nov. Act. Acad. Leop.-Carol. 68: 143. 1897.

Myristica sprucei A. DC. in DC. Prodr. 14: 199. 1856.

Myristica mexicana Hemsl. Biol. Centr.-Am. Bot. 3: 67. 1882.

Compsoneura costaricensis Warb. in Fedde, Repert. Sp. Nov. 1: 71. 1905.

Glabrate shrubs or trees to 13 m., the sap reddish. Leaves chartaceous or subcoriaceous, glabrous, oblong to obovate, apically acute to acuminate, basally attenuate to rounded, 9-30 cm. long, 3.5-10.0 cm. broad; secondary veins (4-)6-10 (-12) on either side; tertiary veins parallel, conspicuously perpendicular to the midrib; petioles 7-30 mm. long, 1-3 mm. broad. Staminate fascicles 3- to 15-flowered, in subspicate racemes (in Panama), the racemes 1-5 per axil, 2-8 cm. long; pedicels 0.5-2.0 mm. long, perianth tardily 3(-4) parted, 1.5-3.0 mm. long, anthers 4-8, 1.0-1.5 mm. long, free or somewhat connate basally, the infra-antheral portion of the column less than 0.5 mm. long. Pistillate fascicles 2-8 cm. long, 1- to 8-flowered; pedicels 2-4 mm. long; perianth accrescent, tardily 3(-4) parted; ovary subglobose, with a subsessile 2-lobed stigma. Fruit somewhat fleshy, ellipsoid, the perianth splitting longitudinally into 2 valves, 20-37 mm. long, 13-21 mm. broad, the reddish aril entire except at the tip.

Southern Mexico to Amazonian Peru and Brazil, at low elevations.

BOCAS DEL TORO: Water Valley, vicinity of Chiriquí Lagoon, *Von Wedel 598, 946, 1717;* vicinity of Chiriquí Lagoon, *Von Wedel 1004, 2382, 2462;* Daytonia Farm, region of Almirante, *Cooper 420;* Changuinola Valley, *Cooper & Slater 84.* COLÓN: Loma de la Gloria, near Fató (Nombre de Dios), 10-104 m., *Pittier 4099, 3846.* SAN BLAS: Permé, *Cooper 241.*

Dr. A. C. Smith observes (in Brittonia 2: 411. 1937) that the Central American material varies from the Amazonian material in having the fascicles subsessile on the rhachis, but he concludes that the variation is of no taxonomic consequence.

3. DIALYANTHERA Warb.

DIALYANTHERA Warb. in Ber. Deutsch. Bot. Ges. 13: 83. 1895, hyponym; in Nov. Act. Acad. Leop.-Carol. 68: 126. 1897.

Dioecious trees often with reddish sap, the younger branchlets pubescent. Leaves alternate, glabrous above, strigillose below with 2- to few-branched hairs, chartaceous or subcoriaceous, petiolate, exstipulate, the tertiary veins obscure. Staminate fascicles in subspicate racemes or subcorymbose, the axes pubescent with few-branched hairs; bracts and bracteoles inconspicuous or absent; flowers 2-40 per fascicle, the perianth deeply but tardily 3(-4)-parted; anthers 2-6, usually free to the base, shorter or longer than the column. Pistillate flowers 2-5 per fascicle, the tepals partially connate; ovary 1-carpellate with a subsessile obscurely 2-cleft stigma. Fruits 1-4 per inflorescence, the ligneous pericarp dehiscing longitudinally into 2 valves; seed ellipsoid to globose, the aril laciniate.

A genus of six species, ranging from Costa Rica through Central America to Amazonian Peru and adjacent Brazil.

a. Petioles winged to the base, 6-14 mm. broad; secondary veins 20-35 on either side; staminate pedicels 5-10 mm. long .....1. D. LATIALATA.

aa. Petioles narrowly if at all winged, 1-6 mm. broad; secondary veins 5-18 on either side; staminate pedicels 1-6 mm. long.

b. Leaves 10-28 cm. long, 4-16 cm. broad, the secondary veins 8-18 on either side; staminate inflorescences subspicate, 3-15 mm. long, the perianth 3.0-4.5 mm. long; androecium 2.4-3.0 mm. long, the anthers attached dorsally at the base .....2. D. OTOBA.

bb. Leaves 5-15 cm. long, 2.5-6.0 cm. broad, the secondary veins 5-10 on either side; staminate inflorescences subcorymbose, 1.0-2.5 cm. long, the perianth 1.5-3.0 mm. long; androecium 1.7-2.1 mm. long, the anthers attached dorsally near the middle .....3. D. ACUMINATA.

1. DIALYANTHERA LATIALATA Pittier, in Contr. U. S. Nat. Herb. 20: 454, 1922.

Dioecious trees to 20 m., the younger branchlets strigillose, glabrescent. Leaves rugulose, minutely strigillose below, elliptic or obovate-elliptic, apically cuspidate or short-acuminate, basally attenuate, 20-40 cm. long, 7-13 cm. broad; secondary veins 20-25 on either side, the tertiary veins obscure; petioles winged, 15-40 mm. long, 6-14 mm. broad. Staminate fascicles in subspicate racemes, the racemes 1-3 per axil, 10-16 cm. long; fascicles 10- to 40-flowered, the pedicels 5-10 mm. long; perianth tardily 3-parted, 2.5-3.5 mm. long; bracts deciduous; anthers 2-3, ca. 0.25 mm. long, free to their bases, the infra-antheral portion of the androecium ca. 1.5 mm. long. Fruits 2-few per inflorescence, the rugulose ligneous pericarp ultimately splitting longitudinally into 2 valves, compressed-subglobose, short-stipitate, ca. 25 mm. long, 18 mm. broad; seed compressed-subglobose, the aril subentire.

Panama to Colombia, at very low elevations.

CANAL ZONE: forest between Peluca Hydrographic Station and Quebrada Peluca, along R. Boquerón, ca. 70 m., *Steyermark & Allen 17227*. COLÓN: along R. Fató, 10-100 m., *Pittier 4193*.

2. DIALYANTHERA OTOBA (Humb. & Bonpl.) Warb. in Ber. Deutsch. Bot. Ges. 13. 89. 1895.

Myristica otoba Humb. & Bonpl. in Willd. Sp. Pl. 4: 869. 1805.

Dioecious trees to 30 m., the younger branchlets rugulose, strigillose, glabrescent. Leaves verruculose, strigillose but glabrescent below, broadly elliptic to obovate, 10-28 cm. long, 4-16 cm. broad; secondary veins 8-18 on either side, the tertiary veins very obscure; petioles canaliculate, slightly winged, 15-40 mm. long, 1-6 mm. broad. Staminate fascicles in subspicate racemes, 1-3 racemes per axil, 3-16 cm. long; fascicles 2-12, 8- to 15-flowered; pedicels 1-6 mm. long, the fugaceous orbicular bracts 3-4 mm. long; perianth tardily 3-parted, 3.0-4.5 mm. long; anthers 0.5-0.8 mm. long, free to their bases or slightly connate dorsally, the infra-antheral portion of the androecium 1.5-2.5 mm. long. Pistillate flowers 2-5 per fascicle, the perianth 3-lobed nearly to the base, to 5 mm. long; ovary 1-carpellate, with an obscurely 2-lobed stigma on a short curving style. Fruits 2-4 per inflorescence, the verrucose ligneous pericarp dehiscing longitudinally into 2 valves, subglobose to ellipsoid, 21-33 mm. long, 16-23 mm. broad; seed ellipsoid to subglobose, the aril laciniate.

Figure 169. *Dialyanthera latialata*

Costa Rica to Colombia, usually below 1000 m.

BOCAS DEL TORO: vicinity of Guabito, *Stern & Chambers 112;* loc. indet., *Von Wedel 440;* region of Almirante, *Cooper & Slater 7.* CHIRIQUÍ: Progreso, *Cooper & Slater 257* & *451.*

Called *saba, bogamani verde, roble, miguelario*, "wine wood" and "white cedar" in Panama, *fruta dorado* and *sebo* in Costa Rica, and *otoba* in Colombia, this rather large tree has somewhat foul-smelling fruits reputedly used as is the nutmeg. Locally, the wood is utilized in carpentry.

3. DIALYANTHERA ACUMINATA Standl. in Field Mus. Publ. Bot. 4: 209. 1929.

Dioecious trees to 20 m., the younger branchlets strigose, glabrescent. Leaves verrucose, strigillose and glabrescent below, ovate to elliptic, apically acuminate, basally acute or attenuate, 5-15 cm. long, 2.5-6.0 cm. broad; secondary veins 5-10 on either side, the tertiary veins very obscure; petioles canaliculate, 8-20 mm. long, 1-2 mm. broad. Staminate fascicles subcorymbosely disposed, 1-3 "corymbs" per axil, 1.0-2.5 cm. long; fascicles 1-3, 3- to 10-flowered, the pedicels 1-4 mm. long; perianth 1.5-3.0 mm. long, tardily 3- to 4-parted, the bracts to 1 mm. long; anthers 0.25-0.5 mm. long, attached dorsally near the middle, the infra-antheral portion of the androecium ca. 1.5 mm. long. Pistillate and fruiting inflorescences not seen.

Known only from Panama where it is called *saba.*

BOCAS DEL TORO: Daytonia Farm, region of Almirante, *Cooper* 395. COCLÉ: vicinity of El Valle de Antón, ca. 600 m., *Allen 2004;* region north of El Valle de Antón, 1000 m., *Allen* 3645.

4. VIROLA Aubl.

VIROLA Aubl. Pl. Guian. Fr. 2: 904. 1775.

Sebophora Neck. Elem. 2: 188. 1790.

Dioecious shrubs or trees, the younger portions usually pubescent with stellate hairs, the sap often reddish or brownish. Leaves alternate, glabrous above, stellate-pubescent and often glabrescent below, submembranaceous to coriaceous, petiolate, exstipulate, the tertiary veins obscure. Flowers in fascicles, racemes or panicles, the axes usually stellate-pubescent; bracts membranaceous, deciduous; bracteoles absent. Staminate flowers in fascicles of 3-15, the perianth deeply or shallowly 3- to 4-parted; anthers 2-6, dorsally connate, at least basally, longer or shorter than the column. Pistillate flowers solitary or in fascicles of 2-7, the tepals partially connate. Fruits 1-40 per inflorescence, the ligneous pericarp dehiscing longitudinally into 2 valves; seed globose to ellipsoid, the aril laciniate.

The largest American genus, this has 38 species concentrated largely in the Amazon basin. Five of the six Central American species occur in Panama, the sixth being thus far reported only from British Honduras.

a. Hairs of lower leaf surfaces stalked, persistent.
   b. Secondary veins of leaves 10-28 on either side, averaging less than 1 per cm. along the midrib; staminate inflorescences much branched; mature fruits 10-30 per inflorescence, the pericarp 0.5-2.0 mm. thick .....1. V. SEBIFERA.
   bb. Secondary veins of leaves 18-35 on either side, averaging more that 1 per cm. along the midrib; staminate inflorescences 1- or 2-branched; mature fruits 1-5 per inflorescence, the pericarp 2-3 mm. thick .....2. V. KOSCHNYI.

aa. Hairs of the lower leaf surfaces sessile, usually evanescent.

c. Secondary veins of leaves 25-30 on either side, averaging 1.5-2.5 per cm. along the midrib; bracts of the staminate inflorescences 3-5 mm. long; fruits short-stipitate, 3-8 per inflorescence, on pedicels 6-9 mm. long
3. V. NOBILIS.

cc. Secondary veins of leaves 9-21 on either side, averaging 0.8-1.3 per cm. along the midrib; bracts of the staminate inflorescences 2-3 mm. long; fruits sessile.

d. Pedicels of the staminate flowers 0.5-1.5 mm. long, subtended by a conspicuous discoid expansion of the ultimate peduncle; fruits 1-5 per inflorescence, more than 2 cm. long, the pedicels 5-10 long
4. V. GUATEMALENSIS.

dd. Pedicels of the staminate flowers 2-3 cm. long, the subtending peduncle not conspicuously flared in the form of a disk; fruits 5-40 per inflorescence, less than 2 cm. long, the pedicels 2-5 mm. long
5. V. ELONGATA.

1. VIROLA SEBIFERA Aubl. Pl. Guian. Fr. 2: 904. 1775.

Myristica sebifera Sw. Prodr. 96. 1788.
Myristica virola Raeusch. Nom. ed. 3. 292. 1797.
Myristica sebifera var. *cordifolia* A. DC. in DC. Prodr. 14: 195. 1856.
Myristica sebifera var. *curvinervia* A. DC. loc. cit. 1856.
Myristica mocoa A. DC. loc. cit. 1856.
Myristica panamensis Hemsl. Biol. Centr.-Am. Bot. 3: 67. 1882.
Virola sebifera var. *curvinervia* Warb. in Nov. Act. Acad. Leop.-Carol. 68: 174. 1897.
Virola venezuelensis Warb. loc. cit. 182. 1897.
Virola mocoa (A. DC.) Warb. loc. cit., 183. 1897.
Virola boliviensis Warb. loc. cit. 184. 1897.
Virola panamensis (Hemsl.) Warb. loc. cit. 185. 1897.
Virola peruviana var. *tomentosa* Warb. loc. cit. 189. 1897.
Virola mycetis Pulle, in Rec. Trav. Bot. Néerl. 4: 125. 1907. in part.
Virola warburgii Pittier, in Contr. U. S. Nat. Herb. 18: 143. 1916.

Dioecious, often buttressed trees to 40 m., the younger branchlets persistently tomentose or glabrescent. Leaf blades glabrous above, with persistent, ochraceous stalked-stellate hairs below, coriaceous, oblong to elliptic-ovate or obovate, acute to acuminate, cordate, truncate or acute, 10-47 cm. long, 4-15 cm. broad; secondary veins 10-28 per side, averaging less than 1 per cm. along the midrib, the tertiary veins rather prominent below; petioles canaliculate, 8-25 mm. long, 2-5 mm. broad. Staminate flowers in much-branched panicles; pedicels 0-3 mm. long; bracts inconspicuous or absent; perianth tardily 3(-5)-lobed, 1.3-3.0 mm. long; anthers 3(-5), 0.7-1.5 mm. long, usually connate to the apex, the infra-antheral portion of the androecium 0.2-1.0 mm. long. Pistillate flowers solitary or clustered in racemes 3-7 cm. long, 2-7 cm. broad; pedicels 1-4 mm. long; tepals partially connate, with subpinnate ochraceous pubescence; ovary 1-carpellate, with a sessile, obscurely 2-lobed stigma. Fruits 10-30 per inflorescence, the velutinous ligneous pericarp ultimately dehiscing longitudinally into 2 valves, subglobose to ellipsoid, 10-21 mm. long, 7-17 mm. broad; seed ellipsoid to subglobose, the aril laciniate.

Nicaragua to southern Brazil, Bolivia and Peru, usually below 1500 m.

BOCAS DEL TORO: region of Almirante, *Cooper 648*. CANAL ZONE: Barro Colorado Island, Barbour Point to next point south, *Bangham 493*, Barro Colorado Island, *Dwyer 1440;* Barro Colorado Island, *Ebinger 300*, *Kenoyer 361*, *493;* Barro Colorado Island, Gatún Lake, *Standley 31287*, *31440*, *41091;* road along R. Pina-R. Media divide, *Johnston 1601*, *1602*. CHIRIQUÍ: Comarca del Barú, area w. of Puerto Armuelles, 100 ft., *Stern & Chambers 128;* vicinity of San Félix, 0-120 m., *Pittier 5255*. DARIÉN: shores of Bahía de Piñas, *Stern & Chambers 194;* vicinity of Campamento Buena Vista, R. Chucunaque, above confluence with R. Tuquesa, *Stern, Chambers et al 881;* vicinity of Cana, 1750 ft., *Stern, Chambers et al 512;* vicinity of La Palma, 0-50 m., *Pittier 6615*. PANAMÁ: Cerro Azul, *Dwyer 1383;* forest along R. Chagres above Alhajuela, *Pittier 3505;* Juan Díaz, *Standley 30615;* R. Tecumen, *Standley 29373;* R. Tapía, *Standley 28249*.

Colloquial names reported in Panama are *malagueta de montana, mancha, bogamani* and *fruta dorado*.

Stern & Chambers 194 and *Kenoyer 361* approach *V. guatemalensis* in that the subsessile stellate hairs are rather fugaceous, but A. C. Smith (in Brittonia 2: 468. 1937) reveals that Central American specimens of *V. sebifera* deviate from Amazonian specimens in having larger fruits and more pronounced tendencies towards glabrescence and acute rather than cordate leaf bases. Warburg (in Nov. Act. Acad. Leop.-Carol. 68: 171. 1897) explains that many of the economic uses attributed to this species may be due to confusion with other members of the family.

2. VIROLA KOSCHNYI Warb. in Fedde, Repert. Sp. Nov. 1: 71. 1905.

Virola merendonis Pittier, in Contr. U. S. Nat. Herb. 20: 453. 1992.

Dioecious trees to 40 m., the younger branchlets densely tomentose to hirsute with ochraceous, usually evanescent hairs. Leaves glabrescent above except for the midrib, with persistent, ochraceous, stalked-stellate hairs below, coriaceous, oblong to narrowly ovate or obovate, apically acuminate or attenuate, basally cordate to acute, 13-38 cm. long, 4-13 cm. broad; secondary veins 18-35 on either side, averaging more than 1 per cm. along the midrib, the tertiary veins rather prominent below; petioles canaliculate, 7-16 mm. long, 1.5-4.0 mm. broad. Staminate flowers in few-branched panicles, the pedicels 1-5 mm. long; bracts ca. 5 mm. long, deciduous; perianth tardily 3-parted, 1.5-3.0 mm. long; anthers 3, 0.6-0.9 mm. long, usually connate to the apex, the infra-antheral portion of the androecium 0.5-1.2 mm. long. Pistillate flowers in clusters of 3-7 in racemes to 5 cm. long; pedicels 0.5-3 mm. long; tepals connate, with simple or few-branched hairs, the 1-carpellate ovary with a subsessile obscurely 2-cleft stigma. Fruits 1-5 per inflorescence, on pedicels 5-8 mm. long, the glabrescent ligneous pericarp ultimately dehiscing longitudinally into 2 valves, subglobose to ellipsoid, 18-30 mm. long, 16-21 mm. broad; seed ellipsoid to subglobose, the aril laciniate.

Guatemala to Panama.

CHIRIQUÍ: Progreso, *Cooper & Slater 175;* Almirante region, *Cooper & Slater 24*. DARIÉN: foothills of Garagará, Sambú basin, southern Darién, 30-500 m., *Pittier 5623*.

The assignment of *Pittier 5623* to this species is somewhat doubtful. The cuneate leaf bases, with the secondary veins somewhat distantly spaced, suggest a tendency to intergrade with Central American variants of *Virola sebifera*. The specimen certainly departs from typical *Virola koschnyi* and probably merits varietal status, but the thick pericarp of the fruits tends to corroborate its determination as *Virola koschnyi*.

Figure 170. *Virola sebifera*

3. Virola nobilis A. C. Smith, in Brittonia 2: 490. 1937.

Dioecious trees to 65 m., the younger branchlets sparsely puberulent with canescent hairs, glabrescent. Leaves glabrous above, with fugaceous canescent sessile-stellate hairs below, coriaceous, narrowly oblong, apically short-acuminate, basally acute to attenuate, 9-16 cm. long, 2.3-4 cm. broad, the secondary veins 25-30 per side, the tertiary veins rather obscure; petioles canaliculate, puberulent, 5-10 mm. long, 1-2 mm. broad. Staminate fascicles in panicles up to 4 cm. long, the bracts deciduous, 3-5 mm. long; anthers 3, ca. 0.8 mm. long, connate to apex, the infra-antheral portion of the androecium 0.1-0.3 mm. long. Pistillate flowers in clusters of 3-several in racemes up to 5 cm. long, the connate tepals densely puberulent with much-branched hairs; ovary 1-carpellate, with a subsessile obscurely 2-cleft stigma. Mature fruits 3-8 per inflorescence; pedicels 6-9 mm. long; pericarp densely puberulent, ultimately dehiscing longitudinally into 2 valves, short-stipitate, ellipsoid, 19-32 mm. long, 14-22 mm. broad; aril laciniate, the seed ellipsoid.

Known only from the Canal Zone and adjacent Panama.

canal zone: back of clearing at laboratory, Barro Colorado Island, *Wetmore, Abbe & Shattuck 155;* hills north of Frijoles, *Standley 27507;* Barro Colorado Island *Aviles 29;* clearing, Barro Colorado Island, *Shattuck 694;* Barro Colorado Island, *Carpenter 43.* panamá: Cerro Azul, *Dwyer 1530.*

4. Virola guatemalensis (Hemsl.) Warb. in Nov. Act. Acad. Leop.-Carol. 68: 220. 1897.

Myristica guatemalensis Hemsl. Biol. Centr.-Am. Bot. 3: 66. 1882.

Virola laevigata Standl. in Field Mus. Publ. Bot. 4: 209. 1929.

Dioecious trees to 30 m., the younger branchlets puberulent with evanescent ferruginous or cinereous hairs. Leaves glabrous above, sparsely puberulent with fugaceous sessile-stellate hairs below, coriaceous, oblong to narrowly obovate, apically acuminate or cuspidate, basally attenuate to obtuse, 13-25 cm. long, 4-8 cm. broad; secondary veins 14-21 per side, the tertiary veins rather obscure; petioles canaliculate, 5-14 mm. long, 1-3 mm. broad. Staminate fascicles in many-flowered panicles 5-12 cm. long and nearly as broad; pedicels 0.5-1.5 mm. long, subtended by a conspicuous discoid expansion of the peduncle; bracts deciduous, 2-3 mm. long; perianth tardily 3-parted, ca. 2 mm. long; anthers 3, 0.6-0.8 mm. long, connate to apex, the infra-antheral portion of the androecium 0.4-0.7 mm. long. Pistillate flowers in few-flowered racemes 5-9 cm. long; tepals densely tomentose with ferruginous stellate or branched, fugaceous hairs; ovary 1-carpellate with a subsessile obscurely 2-cleft stigma. Fruits 1-5 per inflorescence; pedicels 5-10 mm. long, the glabrescent, ligneous pericarp ultimately dehiscing longitudinally into 2 valves, ovoid-ellipsoid, 27-36 mm. long, 21-27 mm. broad; aril deeply laciniate, the seed ellipsoid.

Guatemala to western Panama.

chiriquí: Progreso, *Cooper & Slater 308.*

Standley and Steyermark (in Field Mus. Publ. Bot. 24[4]: 298. 1946) report several uses for this species in Guatemala: the seeds are employed in flavoring

beverages, oil expressed from the seeds is utilized in candle-making, and branches with the characteristic whorl of branchlets are used as egg beaters. A. C. Smith (in Brittonia 2: 499. 1937) lists *cacao volador, quieche, sangre fruta dorado* and *bogamani* as common names for this Central American species.

5. VIROLA ELONGATA (Benth.) Warb. in Ber. Deutsch. Bot. Ges. 13: 89. 1895, hyponym; in Nov. Act. Acad. Leop.-Carol. 68: 178. 1897.

Myristica elongata Benth. in Hooker's Journ. Bot. & Kew Misc. 5: 5. 1853.
Myristica punctata Benth. loc. cit. 6. 1853.
Myristica theiodora Benth. loc. cit. 1853.
Myristica cuspidata var. *rufula* A. DC. in DC. Prodr. 14: 696. 1857.
Virola elongata var. *punctata* (Benth.) Warb. in Nov. Act. Acad. Leop.-Carol. 68: 179. 1897.
Virola elongata var. *longicuspis* Warb. loc. cit. 1897.
Virola elongata var. *subcordata* Warb. loc. cit. 180. 1897.
Virola rufula Warb. loc. cit. 181. 1897.
Virola theiodora (Benth.) Warb. loc. cit. 187. 1897.

Dioecious shrubs or small trees to 25 m., the younger branchlets puberulent with ochraceous evanescent hairs. Leaves glabrous above, sparsely puberulent below with fugaceous sessile stellate hairs, subcoriaceous, apically acute to acuminate, basally obtuse to acute, 7-32 cm. long, 1.5-11.0 cm. broad; secondary veins 9-20 per side, the tertiary veins obscure; petioles canaliculate, 4-16 mm. long, 1.0-2.5 mm. broad. Staminate fascicles in broad many-flowered panicles 4-18 cm. long, 3-15 cm. broad; pedicels 2-3 mm. long, the subtending peduncle not conspicuously expanded; bracts deciduous, 2-3 mm. long; perianth tardily 3(-4) parted, 1.5-3.0 mm. long; anthers 3(-6), 0.6-1.6 mm. long, connate to apex or distally divergent, the infra-antheral portion of the androecium 0.2-0.6 mm. long. Pistillate flowers few in racemes 4-7 cm. long; tepals densely tomentose with ochraceous, stellate fugaceous hairs; ovary 1-carpellate with a subsessile, obscurely 2-cleft stigma. Fruits 5-40 per inflorescence; pedicels 2-5 mm. long, the glabrescent ligneous pericarp ultimately dehiscing longitudinally into 2 valves, ellipsoid or subglobose, 11-16 mm. long, 8-12 mm. broad; aril deeply laciniate, the seed ellipsoid.

Panama to Amazonian Brazil and Peru.

CANAL ZONE: area west of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1796.*

The fruits of the Panama specimen are apparently malformed but the indument and venation of the leaves compare favorably with more southern representatives of the species, formerly not known from Central America.

MONIMIACEAE

By J. A. DUKE

Aromatic, often lemon-scented shrubs or small trees. Leaves mostly opposite, rarely ternate or subalternate, exstipulate, penninerved, entire or irregularly dentate, membranaceous to coriaceous, glabrous to densely pubescent with simple or stellate hairs. Flowers unisexual (in America), perigynous, mostly dioecious, actinomorphic or asymmetrical, in axillary dichotomous or trichotomous cymes or rarely solitary,

the pedicellate hypanthia urceolate to campanulate. Staminate flowers with few to several tepals, these usually uniseriate, often reduced to a subentire annulus encircling the hypanthium; stamens 2-many, the outer often broader and occasionally sterile, the anthers oblong and valvate, or hippocrepiform and longitudinally dehiscent (in North America), the filaments occasionally with a pair of lateral appendages; pistillodes usually absent. Carpellate flowers usually fewer and larger than the staminate; tepals 4-several, occasionally caducous and leaving a repand discoid hypanthium exposing the several separate carpels, more frequently persistent at the summit of the fleshy hypanthium tube (valve) in which the carpels are permanently imbedded. Fruiting carpels several, 1-seeded, free or imbedded in the hypanthium, the seeds mostly erect in the drupaceous or coriaceous carpels.

Confined largely to the tropics of both hemispheres, this family of some 30 genera is represented in North America by only 2. In the Americas the family is of only casual economic importance, with the Brazilian *Mollinedia schottiana* (Spreng.) Perk. and the Chilean *Peumus boldus* Mol. finding a limited demand in the timber trade. Some aromatic species are used in making teas supposed to have medicinal virtues. Considerable phylogenetic significance has been attributed to the combination of magnoliaceous and lauraceous characters in the family, which, according to the anatomical findings of Garratt (in Trop. Woods 39: 18. 1934), is more nearly lauraceous.

Specific determinations in the American representatives are very difficult and a revision of existing specific concepts will ultimately be necessary. If one adopts the narrow concept followed by Perkins (in Engl. Pflanzenreich 4. Fam. 101. 1901), he will discover still many undescribed species in the Americas. Too often Perkins' key characters are based on indumental and numerical variations. More reliable characters should be incorporated into a much-needed reorganization of this puzzling family.

a. Anthers oblong, valvately dehiscent; tepals of the pistillate flowers 4-several, usually persistent, the fruits enclosed in the hypanthium; leaves glabrous or with simple or stellate hairs ..... 1. Siparuna.

aa. Anthers hippocrepiform, longitudinally dehiscent; tepals of the pistillate flowers 4, soon deciduous, the fruits not enclosed in the hypanthium; leaves glabrous or with simple hairs ..... 2. Mollinedia.

1. SIPARUNA Aubl.

Siparuna Aubl. Hist. Pl. Guian. Fr. 2: 864. 1775.

Citrosma Ruiz & Pavón, Fl. Per. & Chil. Prodr. 134. 1794.

Leonia Mutis, ex Kunth, Synops. Pl. 1: 462. 1822.

Conuleum A. Rich. in Act. Soc. Hist. Nat. Paris 1: 391. 1823.

Citriosma Tul. Monogr. 311. 1855.

Angelina Pohl, ex Tul. loc. cit. 363. 1855.

Dioecious or monoecious aromatic shrubs or small trees. Leaves usually opposite, glabrous to densely hairy, the hairs simple or stellate, the blades membrana-

ceous to pergameneous, entire to irregularly dentate. Flowers pedicellate to subsessile, usually in axillary dichotomous or trichotomous cymes, the hypanthium often surmounted by an annular fusion of the tepal bases. Staminate flowers 3-many, with 4-8 subequal exappendiculate tepals united below to form an annulus interior to which is often a flat or hemispherical, apically perforate velum; stamens 1-many, scattered or in circular disposition, the filaments often dilated or conduplicate, the anthers oblong, valvate. Carpellate flowers similar to the staminate but usually fewer and larger; annulus and velum often present; carpels 4-many, the styles elongate, usually exserted, often basally connate. Fruits drupaceous or coriaceous, permanently enclosed in the accrescent hypanthium; seeds tuberculate, ultimately exposed by the irregular bursting of the aggregate fruit.

A puzzling economically trivial genus of about 100 "species," at least 8 of them found in Panama. Several others are to be found in northern Central America and Mexico, but far more occur in South America.

a. Lower leaf surfaces, young twigs and outer surfaces of the tepals hirsute or densely tomentose with a matted indument; plants dioecious; stamens 4-31.

b. Stamens 8-30; leaves tomentose with a velvety indument, mostly 8-16 mm. broad ..... 1. S. PAUCIFLORA.

bb. Stamens 4-6; leaves hirsute or, if tomentose, less than 8 cm. broad:

c. Leaves tomentose, equilateral, entire or minutely denticulate. 2. S. GRISEO-FLAVESCENS.

cc. Leaves hirsute, often falcate, denticulate, some of the teeth at least 1 mm. long ..... 3. S. TONDUZIANA.

aa. Lower leaf surfaces, young twigs and outer surfaces of the tepals glabrous or with scattered appressed stellate hairs; plants dioecious or monoecious; stamens 2-14:

d. Leaves pergameneous, entire; plants monoecious; stamens (8-)10-14; velum lacking, the tepals erect, usually obscure in fruit ..... 4. S. GUIANENSIS.

dd. Leaves membranaceous, if pergameneous denticulate; plants dioecious; stamens 2-8; velum present, the tepals erect or reflexed, usually obvious in fruit:

e. Stamens 4-8; leaves denticulate or, if entire, mostly more than 8 cm. long:

f. Leaves denticulate; outer circle of stamens separate or connivent:

g. Outer circle of stamens connivent; leaves equilateral, 10-20 cm. long ..... 5. S. TETRACEROIDES.

gg. Outer circle of stamens not connivent; leaves falcate, mostly 5-10 cm. long ..... 6. S. RIPARIA.

ff. Leaves entire, outer circle of stamens not connivent 7. S. NICARAGUENSIS.

ee. Stamens 2; leaves entire, less than 8 cm. long ..... 8. S. DIANDRA.

1. SIPARUNA PAUCIFLORA (Beurl.) A. DC. in DC. Prodr. 16²: 696. 1868.

Citriosma pauciflora Beurl. in Vet. Akad. Handl. Stockh. 1854: 144. 1856.

Siparuna cauliflora Hemsl. Biol. Centr.-Am. Bot. 3: 69. 1882.

Dioecious aromatic shrubs or small trees to 10 m., often branching from the base, the ultimate branchlets terete to quadrangular, gray-tomentose, the hairs to

0.5 mm. long. Leaves opposite, membranaceous to subpergameneous, narrowly elliptic to obovate, apically acute to acuminate, basally cuneate to rounded, coarsely serrate to almost entire, densely gray stellate-tomentose below, densely to sparsely so above, the hairs to 0.8 mm. long; blades (10-)15-40 cm. long, (6-)8-16 cm. broad, with 10-16 pairs of lateral veins, the canaliculate petioles 1-6 cm. long. Staminate inflorescence of 5- to 15-flowered subsessile axillary cymes, often cauliflorous, gray to yellow stellate-pubescent throughout; peduncles, 1-6 mm. long; pedicels 2-10 mm. long; tepals connate, forming an undulate subentire annulus; velum conical, 4-5 mm. in diameter, the apical pore 1.0-1.5 mm. in diameter; stamens (8-)12-30, the outermost filaments dilated, ovate to orbicular, ca. 1 mm. long, the valvate anthers minute, introrse, usually slightly exserted. Carpellate inflorescences similar to the staminate but the cymes usually sessile, the 3-15 pedicels 2-10 mm. long; tepals connate forming an undulate annulus, the velum ultimately concave, the many separate styles scarcely exserted through the orifice. Aggregate fruits ecallose, globose, capped by the persistent annulus, yellowish-green, drying black, 10-15 mm. in diameter, bursting irregularly exposing the pinkish interior and the several tuberculate seeds.

Peru to Colombia and Costa Rica, mostly at low elevations; called *limoncillo* in Costa Rica.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *Von Wedel 162, 1968, 2085, 2165;* Almirante region, *Cooper & Slater 69;* Daytonia Farm, region of Almirante, *Cooper 422;* Farm Six, Changuinola valley, *Dunlap 489.* CANAL ZONE: Mojinga Swamp near mouth of R. Chagres, below 1 m., *Allen 908;* Barro Colorado Island, *Ebinger 62, Kenoyer 469, Standley 31297, 31301, 31428, 40854, Wilson 32;* Chagres, Isthmus of Panama, *Fendler 196;* Gatún, *Sutton Hayes s. n.;* area west of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1711;* 1-3 mi. from Gorgona above the reservoir, 40-150 m., *Maxon 4742;* vicinity of Frijoles, *Piper 5283;* near old Fort Lorenzo, mouth of R. Chagres, *Piper 5913;* around Las Cruces, 20-100 m., *Pittier 2620;* along Caño Quebrado, *Pittier 6660.* COCLÉ: north rim of El Valle de Antón, 600-1000 m., *Allen 1636.* COLÓN: forests around Porto Bello, 5-100 m., *Pittier 2430;* between France Field, Canal Zone and Cativa1, Province of Colón, *Standley 30300.* DARIÉN: banks of Río Paca, *Stern, Chambers et al 715;* vicinity of Campamento Buena Vista, R. Chucunaque above confluence with R. Tuquesa, *Stern, Chambers et al 829;* Cana-Cuasi Trail (Camp 2), Chepigana, 2000 ft., *Terry & Terry 1474.* PANAMÁ: Cerro Azul, *Dwyer 1523;* R. Tecumen, *Standley 26752, 29348;* R. Tapía, *Standley 28265;* Juan Díaz, *Standley 30588.*

2. SIPARUNA GRISEO-FLAVESCENS Perk. in Engl. Bot. Jahrb. 38: 693. 1901.

Dioecious shrubs 2-3 m. high, the ultimate branches terete and densely yellowish- or grayish-tomentose, the hairs ca. 0.5 mm. long. Leaves opposite, membranaceous, densely yellow stellate-tomentose below, scantily so above, the hairs ca. 0.5 mm. long; blades oblong to obovate, apically acuminate, basally rounded to subcordate, entire or minutely denticulate, 10-17 cm. long, 4-8 cm. broad, with 9-11 pairs of secondary veins, the canaliculate petioles 1-4 cm. long, densely yellow-tomentose. Staminate inflorescences of 2- to 8-flowered axillary corymbiform cymes, yellow-tomentose except for the velum; peduncles ca. 5 mm. long, the pedicels ca. 1 mm. long; tepals 4, minute, rounded, glabrous within; velum more or less flat, 3-5 mm. in diameter, the aperture ca. 1 mm. in diameter; stamens 6, exserted, the outermost much broader than the innermost. Carpellate in-

florescences of usually 2 2- to 4-flowered cymes in each axil, densely yellow-tomentose except for the velum, the peduncles 2-4 mm. long, the pedicels 2-3 mm. long; tepals connate forming an entire or undulate repand annulus; velum convex, ca. 3 mm. in diameter, the aperture ca. 1 mm. in diameter, the 12-18 styles clearly exserted and tending to be connate at the aperture. Fruits not seen ("red" *fide* Standley, in Field Mus. Publ. Bot. 18²: 449. 1937.)

Costa Rica to Panama.

CHIRIQUÍ: between Hato del Jobo and Cerro Vaca, eastern Chiriqui, 700-1000 m., *Pittier 5404.*

The specimen cited, determined by Standley as *S. griseo-flavescens*, is carpellate, but agrees well with Perkins' description of the species, based on a staminate plant (*Pittier 1879* from Costa Rica). *Siparuna patelliformis* Perk. would seem to be very closely allied indeed.

3. SIPARUNA TONDUZIANA Perk. in Engl. Bot. Jahrb. 31: 746. 1902.

Dioecious aromatic shrubs or small trees to 8 m., the ultimate branches terete, reddish-brown, hirsute with yellow to orange, mostly simple hairs to 3 mm. long. Leaves opposite, membranaceous, densely hirsute, at least below, with mostly simple hairs to 3 mm. long; blades elliptic to oblong-obovate, mostly inequilateral, apically long-acuminate, basally cuneate to cordate, coarsely and irregularly denticulate, 8-28 mm. long, 4-10 mm. broad, with 10-15 pairs of secondary veins, the terete to canaliculate petioles 0.5-3 cm. long. Staminate inflorescences usually 2 in each axil, corymbiform, with 3-7 flowers, or subspiciform with 3-15 flowers, the branching often unequal, yellow-pubescent throughout except for the velum; peduncles 4-15 mm. long, the pedicels 0-6 mm. long; tepals mostly 5-6, minute, ultimately forming a repand undulate annulus, the velum convex, 3-4 mm. in diameter, the aperture 1-1.5 mm. in diameter; stamens mostly 6, separate, the outer 4 broader and flatter, usually exserted, ca. 1 mm. long, the valvate anthers minute, introrse. Carpellate inflorescences like the staminate but the flowers usually fewer and slightly larger; styles 8-20, connivent near the apical aperture. Aggregate fruits callose, subreniform, capped by the minute lobate annulus, pinkish-red, ca. 10 mm. long and 15 mm. broad, bursting irregularly and exposing the pinkish interior and the tuberculate seeds.

Panama to Guatemala, where it is called colloquially *salvia* and *cerbatanero.*

BOCAS DEL TORO: Cricamola Valley, region of Almirante, *Cooper 194;* Buena Vista Camp on Chiriquí Trail, region of Almirante, alt. 1250 ft., *Cooper 596;* without locality, *Von Wedel 170.*

4. SIPARUNA GUIANENSIS Aubl. Hist. Pl. Guian. Fr. 2: 865. 1775.

Citrosma discolor Poepp. & Endl. Nov. Gen. & Sp. 2: 48. 1817.

Citriosma guianensis (Aubl.) Tul. Monogr. 361. 1855.

Cistriosma guianensis β *nuda* Tul. loc. cit. 362. 1855.

Citriosma guianensis γ *divergentifolia* Tul. loc. cit. 1855.

Siparuna panamensis A. DC. in Journ. Bot. 3: 219. 1865.
Siparuna discolor A. DC. in DC. Prodr. 16²: 656. 1868.
Siparuna guianensis β *glabrescens* A. DC. loc. cit. 654. 1868.
Siparuna guianensis γ *longifolia* A. DC. loc. cit. 1868.
Siparuna guianensis δ *divergentifolia* A. DC. loc. cit. 1868.
Siparuna foetida Barb. Rodr. in Vellosia 2¹: 68. 1891.
Siparuna guianensis var. *nitens* O. Ktze. Rev. Gen. 3²: 276. 1898.

Monoecious aromatic shrubs or trees to 20 m., the ultimate branches terete or slightly flattened, reddish to greenish-brown, tomentose or glabrescent. Leaves opposite, pergameneous, mostly appressed-strigillose and glabrescent above, stellate-pubescent and glabrescent below; blades oblong to elliptic, apically acute to long-acuminate, basally cuneate to truncate, entire, usually symmetrical, 5-25 cm. long, 3-10 cm. broad, with 7-11 lateral veins on each side, the petioles 5-10(-15) mm. long. Staminate inflorescences hermaphroditic or unisexual, of 2-4 3- to 21-flowered cymes in each axil, yellow stellate-pubescent throughout, often with one conspicuous dichotomous branch to the peduncle, the unbranched portion to 15 mm. long, the pedicels to 3 mm. long; tepals 4-6, deltoid to somewhat hemispherical, the velum lacking; stamens (8-)10-14. Carpellate inflorescences similar to the male, the flowers with several long-exserted, basally connate styles, the velum, if present, obscured by the tepals, conical. Aggregate fruits callose, contorted, obscuring the tepals, pinkish, 8-14 mm. long, 8-14 mm. broad, bursting irregularly and exposing the yellowish interior with its few tuberculate grayish seeds.

Peru and Brazil to Colombia and Costa Rica.

CANAL ZONE: Barro Colorado Island, *Aviles 16, Bangham 457, Shattuck 793, 1074;* Chagres, Isthmus of Panama, *Fendler 188;* area w. of Limón Bay, Gatún Locks and Gatún Lake, road along R. Pina-R. Media divide, *Johnston 1808;* near Ft. Randolph, *Maxon & Harvey 6525;* vicinity of Miraflores Lake, *Peggy White 250.* CHIRIQUÍ: vicinity of San Félix, 100 m., *Allen 3654.* DARIÉN: vicinity of La Palma, 0-50 m., *Pittier 6699.* HERRERA: Ocú, *Ebinger 1091.* PANAMÁ: La Campana, Cerro Campana, *Ebinger 336;* R. Tapía, *Standley 28093, 28296.* VERAGUAS: San Francisco, *Dwyer 1280.*

Standley (in Contr. U. S. Nat. Herb. 27: 182. 1928) reports that in Panama, where it is called *hierba de pasmo*, the plant is supposed to be used as a remedy for colic and as a vermifuge on fowl. This is the only confirmedly monoecious species of the Monimiaceae in Central America, but, when the monoecious condition is not obvious, it is difficult to distinguish from *S. nicaraguensis.*

5. SIPARUNA TETRACEROIDES Perk. in Engl. Bot. Jahrb. 28: 689. 1901.

Dioecious shrubs or small trees, the branchlets terete, reddish, with gray hairs to 0.4 mm. long. Leaves opposite, the blades membranaceous, narrowly elliptic to obovate, apically with a mucronate or emarginate acumen, basally cuneate, marginally undulate-denticulate, 8-20 cm. long, 5-8 cm. broad, glabrescent above, scantily stellate-pilose below, with 8-12 pairs of arcuately ascending veins, the petiole gray-pilose, 2-5 cm. long. Staminate inflorescences of few-flowered cymes mostly paired in the axils of the leaves, with gray stellate hairs, the peduncles

Figure 171. *Siparuna tetraceroides*

2-4 mm. long, the pedicels 1-3 mm. long; flowers rotate, ca. 2 mm. in diameter, the receptacle obconic, the tepals obsolescent, ultimately connate and repand, the velum hemispheric, the orifice ca. 1 mm. in diameter, stamens 5-8, the 4 exterior in a whorl and often connate or connivent, 1.5-2.2 mm. long, the anthers minute, introrse, exserted. Carpellate inflorescences similar to the staminate, perhaps fewer-flowered, the tepals obscure, deltoid, ultimately forming an undulate annulus, the styles more or less connivent at the aperture. Fruits callose, reniform, capped by the persistent tepals.

Costa Rica to western Panama.

CHIRIQUÍ: between El Hato (Volcán) and Costa Rica, *Ebinger 813;* Puerto Remedios, 0-30 m., *Pittier* 3386; in forest, Cerro de la Plata, near San Félix, eastern Chiriquí, 12-150 m., *Pittier 5156.*

The cited Panama specimens depart rather radically from Costa Rican material and might be deserving of some nomenclatural status. Panama material has more delicate, less coarsely toothed leaves, and the veins are not so conspicuously yellow as those specimens from Costa Rica which I believe to be properly called *S. tetraceroides* (*Pittier 16144*, cited by Perkins, and *Skutch 2220*, 3813, 3985). The staminate Panama plant (*Pittier 5156*), illustrated in Fig. 171, has the outer whorl of stamens connate, and in this respect represents an approach to the Colombian *S. steleandra* Perk.

6. Siparuna riparia (Tul.) A. DC. in DC. Prodr. 16²: 647. 1868.

Citriosma riparia Tul. in Ann. Sci. Nat. 4³: 36. 1855.
Siparuna riparia var. *macrophylla* Perk. in Engl. Bot. Jahrb. 28: 690. 1901.
Siparuna riparia var. *grandiflora* Perk. in Engl. Pflanzenr. 4. Fam. 101: 99. 1901.
Siparuna riparia var. *calantha* Perk. in Notizbl. Bot. Gart. Berl. 10: 164. 1927.

Dioecious shrubs or small trees to 6 m., the ultimate branches terete or quadrangular, reddish-brown or gray, tomentose with yellowish or grayish stellate hairs to 1 mm. long. Leaves opposite, membranaceous, pilose, especially below, with stellate hairs to 1 mm. long; blades elliptic to obovate, often inequilateral, apically acute to caudate-acuminate, basally cuneate to truncate, serrate, 5-12 mm. long, 3.5-6.0 cm. broad, with 8-10 lateral veins on either side, the subterete to canaliculate petioles 1.0-3.5 cm. long. Staminate inflorescences of 2-3 3- to 15-flowered cymes in each axil, grayish to yellowish stellate-pubescent except for the velum; peduncles mostly 4-10 mm. long before branching, the pedicels 3-12 mm. long; tepals 4-7, at first triangular, ultimately rounded and somewhat reflexed; stamens mostly 5-6, the outer 4 disposed in a circle but not connate; velum ca. 2 mm. in diameter, the orifice ca. 1 mm. in diameter. Carpellate inflorescences similar to the staminate, the styles 6-12, connate near the orifice, long-exserted. Aggregate fruits callose, reniform, reddish, ca. 10 mm. broad, 10-15 mm. broad.

Mexico to Colombia.

CHIRIQUÍ: rain forest, Bajo Chorro, 6000 ft., *Davidson 242;* vicinity of Bajo Mona and Quebrada Chiquero, 1500 m., *Woodson & Schery 600.*

The identity of the cited specimens is not without question. Although Perkins has said that the stamens are 10-12 in *S. riparia, Bourgeau 1748,* identified by Perkins as *S. riparia,* has 5-6 stamens, and I believe the latter numbers to be more prevalent.

7. Siparuna nicaraguensis Hemsl. Biol. Centr.-Am. Bot. 3: 69. 1882.

Dioecious aromatic shrubs or small trees to 8 m., the ultimate branches terete, ferruginous stellate-pubescent, the hairs evanescent. Leaves opposite, membranaceous, glabrous or subglabrous above, scantily stellate-pubescent to subglabrous below; blades elliptic to obovate, apically more or less acuminate, marginally entire to undulate or minutely denticulate, 6-22 cm. long, 3.5-12.0 cm. broad, with 5-10 lateral veins on either side, the canaliculate petioles 1-9 cm. long. Staminate inflorescences with 1-4 1- to many-flowered cymes in each axil, grayish- to yellowish-puberulent except for the inner portion of the tepals and the velum; peduncles 1-15 mm. long, the pedicels 1-5 mm. long; tepals (3-)4-7, basally connate, the lobes free, rounded or deltoid; velum 2-4 mm. broad, the pore ca. 1 mm. in diameter; stamens 5-8, the outer 4 or 5 separate, occasionally disposed in a circle embracing the inner 1-3 which are often conduplicate, ca. 1 mm. long; anthers valvate, minute, introrse. Carpellate inflorescences similar to the staminate but with fewer flowers, only 1 in a given cyme usually developing into fruit, the numerous styles exserted ca. 0.5 mm. Aggregate fruits smooth or slightly callose, capped by the

Figure 172. *Siparuna nicaraguensis*

persistent erect tepals, orange to red, 10-20 mm. in diameter, bursting irregularly to expose the several tuberculate seeds.

Panama to Mexico.

BOCAS DEL TORO: region of Almirante, *Cooper 616.* COCLÉ: north rim of El Valle, *Allen 1841;* north rim of El Valle de Antón, near Cerro Turega, 650-700 m., *Woodson & Schery 159.* CANAL ZONE: Ancon Hill, *Duke 4610.* COLON: in forest, Loma de la Gloria, near Fató (Nombre de Dios), 10-104 m., *Pittier 4077.* DARIÉN: along the Sambú River, southern Darién, above tide limit, *Pittier 5553;* vicinity of Cana, alt. 1750 ft., *Stern, Chambers et al 468, 690;* Paca, below Cana, *Williams 718.* PANAMÁ: La Campana, Cerro Campana, *Ebinger* 333.

The aromatic leaves of this species, known in various places in Central America as *cerbatana, chuché, hormiguillo, kex, limoncillo, salvia,* "wild coffee" and *yaya de mono,* are locally brewed to form a tea supposedly remedial for respiratory ailments.

Material from Darién, as illustrated in Fig. 172, departs rather disconcertingly from most Central American specimens referred to this species. Both Standley and I have suffered the temptation to treat such Darién material as a new taxon differing from typical *S. nicaraguensis* in having the shorter male tepals subdeltoid and erect at anthesis and uncommonly large leaves and petioles. Such variation is more common to the south but may be found also in specimens from Mexico and northern Central America. It is for that reason that I am reluctant to recognize the variants formally.

Figure 173. *Siparuna diandra*

8. SIPARUNA **diandra** J. Duke sp. nov.

Frutices dioeci 2-4 m. alti ramulis teretibus ferrugineis griseo-pilosiusculis pilis glandulosis ad 0.3 mm. longis. Folia plerumque opposita lamina membranacea obovata vel subelliptica apice caudate acuminata basi attenuata cuneatave utrinque parce stellato-pilosiuscula integra nervis lateralibus plerumque 6-8 arcuate ascendentibus in utroque latere petiolo griseo-pilosiusculo 5-10 mm. longo. Inflorescentiae masculae pauciflorigerae corymbosae in axillis foliorum partibus exterioribus parce grisiter stellateque pilosiusculis pilis ad 0.3 mm. longis pedunculo plerumque 1.0-1.5 mm. longo pedicellis 1.0-3.5 mm. longis. Flores rotati receptaculo obconico ca. 1.0-1.5 mm. in diam. tepalis plerumque 4 triangularibus erectis nigrescentibus ca. 0.5 mm. longis intus glabris; velo tholiforme ore parvissimo staminibus 2 carinatis cucullatisque carnosis glandulosis ad 1.5 mm. longis vix exsertis. Flores feminei nunc ignoti.

DARIÉN: Cana-Cuasi Trail (Camp 2), Chepigana, 2000 ft., Mar. 11, 1940, *Terry & Terry 1496* (HOLOTYPE, MO).

An interesting addition to the flora of Panama, this peculiar species seems to have no close allies in Central America. Among South American species, it would seem to be most closely related to the Peruvian *S. gilgiana* Perk., which differs in having much larger leaves and petioles and the tepals connate into a repand flange, and the Brazilian *S. brasiliensis* Perk., which also has larger leaves, petioles and peduncles.

2. MOLLINEDIA Ruiz & Pavón

MOLLINEDIA Ruiz & Pavón, Fl. Peruv. & Chil. Prodr. 83, *t. 15*. 1794.

Tetratome Poepp. & Endl. Nov. Gen. & Sp. 2: 46, *t. 163*. 1838.

Paracelsia Mart. ex Tul. in Mart. Fl. Bras. 4[1]: 314. 1857.

Dioecious shrubs or small trees. Leaves opposite, glabrous or slightly pilose below, membranaceous to coriaceous, petiolate, exstipulate, entire or irregularly dentate, with few secondary veins confluent at some distance from the margin. Flowers pedicellate, solitary, cymose or corymbiform in the axils, the hypanthium campanulate or urceolate, glabrous or pubescent, the hairs simple. Staminate flowers 3-many per inflorescence, with 4 tepals, the 2 inner frequently smaller and provided with a terminal laciniate appendage; stamens 8-many, included on the inner surface of the hypanthium, the filaments minute, the anthers (in Central America) hippocrepiform, longitudinally dehiscent. Carpellate flowers mostly 1-3 per inflorescence, the 4 petals soon deciduous from the urceolate hypanthium; carpels 6-many, glabrous to pilose, ellipsoid, the styles filiform. Drupes fleshy or coriaceous, sessile or stipitate on the reflexed undulate hypanthium.

With the exception of 1 dubious Australian species, all of the nearly 75 species of this genus are found in tropical and subtropical America. Economically unimportant, the genus is taxonomically perplexing and little can be done to correct this until a monographic study is undertaken. Four of about 15 Central American species occur in Panama.

a. Leaves ovate to obovate, basally rounded to cuneate, weakly toothed; fruits drying black or brown, scarcely stipitate:
   b. Drupes smooth, glabrous, drying black; leaves glabrous, acuminate; branchlets glabrous ..... 1. M. DARIENENSIS.
   bb. Drupes corrugated, often puberulent, drying brown; leaves puberulent, rarely glabrescent, obtuse to shortly acuminate; branchlets pubescent ..... 2. M. COSTARICENSIS.

aa. Leaves lanceolate to rhomb-elliptic, basally cuneate, often strongly toothed; fruits drying brown, occasionally long-stipitate:
   c. Drupes 10-13 mm. long, sessile or obscurely stipitate; leaves membranaceous, usually puberulent; plants dioecious ..... 3. M. PINCHOTIANA.
   cc. Drupes 15-20 mm. long, on stipes 1-3 mm. long; leaves pergameneous, glabrous; plant possibly monoecious ..... 4. M. STIPITATA.

1. MOLLINEDIA DARIENENSIS Standl. in Field Mus. Publ. Bot. 22: 332. 1940.

Dioecious shrubs 1.0-2.5 m. high, the branches glabrous and rather dark in drying. Leaves chartaceous, glabrescent, lance-ovate, apically acuminate, basally cuneate to sub-rounded, 9-16 cm. long, 3-6 cm. broad, with 5-9 irregular teeth on

either side, the secondary veins 4-5 on either side, arcuately anastomosing 2-5 mm. from the margin; petioles ca. 10 mm. long, drying dark brown, glabrous or glabrate. Staminate flowers not known. Carpellate flowers solitary or geminate in the axils of the leaves, the pedicels glabrous or glabrate, ca. 10 mm. long, the peduncles 1-5 mm. long; bracts and bracteoles not apparent; flowers at anthesis not known. Fruits fleshy ellipsoid, rounded at both ends, smooth, drying black, 13-15 mm. long, ca. 10 mm. broad; receptacles reflexed, ca. 10 mm. broad; seeds ca. 12 mm. long, 9 mm. in diameter, the testa mottled.

Panama, known only from the type collection.

DARIÉN: Cana-Cuasi Trail (Camp 2), Chepigana District, 3000 ft., *Terry & Terry 1456*.

2. MOLLINEDIA COSTARICENSIS Donn. Sm. in Bot. Gaz. 33: 257. 1902.

Dioecious shrubs or small trees to 7 m. high, the branchlets pubescent with grayish hairs. Leaves pergameneous, appressed-strigillose, especially below, rarely glabrescent, narrowly to broadly ovate or obovate, apically obtuse to shortly acuminate, basally acute to rounded, 8-18 cm. long, 4-9 cm. broad, subentire or with up to 25 minute irregular teeth on either side, the secondary veins 5-11 on either side, arcuately anastomosing 3-8 mm. from the margin; petioles 5-16 mm. long, drying rufous, puberulent. Staminate inflorescences 1-6 in 3- to 5-flowered cymes in each axil, the bracteate peduncles and pedicels with yellowish puberulence; peduncles 1-20 mm. long, the pedicels 2-5 mm. long. Flowers campanulate, 6-8 mm. in diameter at anthesis; tepals 4, exteriorly with a yellowish puberulence, the inner 2 with an apical laciniate appendage; stamens 16-34, ca. 1 mm. long, the anthers hippocrepiform. Carpellate flowers mostly solitary or paired in the axils, the bracteate peduncles 5-20 mm. long, the bracteolate pedicels to as much as 6 cm. long; flowers turbinate, 2-4 mm. in diameter, the tepals ca. 2 mm. long, caducous, the numerous carpels ellipsoid, with a grayish or yellowish pubescence. Fruiting receptacles discoid, repand, densely strigillose on both surfaces, 10-15 cm. broad; fruits ellipsoid, numerous, brown, corrugated, usually puberulent, 8-13 mm. long, 5-8 mm. broad, the seeds slightly smaller.

Panama and Costa Rica.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete Distr., 6000 ft., *Davidson 370*.

M. costaricensis is not constantly separated from *M. pinchotiana*, but a summation of the following characters seems to define the former rather well: leaves pergameneous, with the lateral veins prominent below, the base rounded, the apex rounded, acute or briefly and abruptly acuminate, the indument yellowish or grayish, the staminate flowers 6-8 mm. in diameter at anthesis, the stamens 16-34.

3. MOLLINEDIA PINCHOTIANA Perk. in Engl. Bot. Jahrb. 31: 743. 1902.

Dioecious shrubs or small trees to 6 m. high, the branchlets often densely puberulent with evanescent brownish hairs. Leaves membranaceous, glabrous or lightly puberulent, narrowly elliptic to obovate, apically acuminate, basally cuneate, with 5-12 irregular arcuate teeth on either side, 5-16 cm. long, 2-6 cm. broad, with

4-5 lateral veins on either side, these conspicuous to inconspicuous below, arcuately anastomosing 2-10 mm. from the margin; petioles 5-18 mm. long, light brown, puberulent or glabrate. Staminate inflorescences 1-4 in the axil of a leaf, usually of 3-flowered cymes, the bracteate peduncles and pedicels with a grayish or reddish-brown puberulence; peduncles 5-20 mm. long, the pedicels 3-30 mm. long. Flowers campanulate, 4-6 mm. in diameter at anthesis; tepals 4, with grayish or reddish-brown puberulence, the inner 2 with a laciniate apical appendage; stamens 23-36 (44 in some Costa Rican deviates with a pinkish puberulence on the leaves), ca. 1 mm. long, the anthers hippocrepiform. Carpellate flowers mostly solitary in the axils, the bracteate peduncles 3-20 mm. long, the bracteolate pedicels 3-30 mm. long; flowers turbinate, 2-3 mm. in diameter, the acute tepals ca. 2 mm. long, promptly deciduous, the numerous carpels ellipsoid, with a grayish puberulence. Fruiting receptacles discoid, reflexed, puberulent on both surfaces, ca. 8-12 mm. broad; fruits ellipsoid, numerous, brown, carnose, 10-12 mm. long, 6-7 mm. broad, the seeds slightly smaller, brown, mottled with purple.

CHIRIQUÍ: humid forest between Alto de las Palmas and top of Cerro de la Horqueta, 2100-2268 m., *Pittier 3246*.

Apparently Standley at one time considered this specimen to represent a new species. The leaves are rather large and basally rounded and the fruits are immature, but the plant appears to be *M. pinchotiana*, a variable species which grades into several "microspecies" in Costa Rica. At one extreme is a "microspecies," apparently unnamed at present, from the region of Zarcero. This is characterized by narrow rhomb-elliptic leaves with a pinkish indument and the stamens numbering about 40. At the other extreme is *M. minutiflora* Standl. & Williams, with multiflorous male inflorescences, the flowers 1.5-2.5 mm. in diameter at anthesis, the stamens 10-16, the leaves glabrous, elliptic and with few or no teeth. Closely allied to *M. mexicana* Perk. (scarcely distinct from *M. nigrescens* Tul.) is a group of specimens from the vicinity of El General, Costa Rica. This group, to which Standley also applied an herbarium name, is characterized by lanceolate leaves with 2-6 teeth on either side, multiflorous staminate inflorescences, the flowers ca. 3 mm. in diameter, the stamens 16-24 in number. Whether all these should be treated as separate species or merely as components of one polymorphic species is a serious question for the monographer.

4. MOLLINEDIA **stipitata** J. Duke, sp. nov.

Frutices dioeci vel interdum fortasse monoeci ad 3 m. alti ramis griseis subteretibus ramulis glabrescentibus griseis vel rufis. Folia opposita lamina glabra anguste lateve elliptica apice acuta vel acuminata basi cuneata vel acuta in utroque margine denticulata dentibus aristatis 1-5 irregulariter remotis 6-11 cm. longa 15-45 mm. lata utrinque glabra nervis prominentibus lateralibus plerumque 5 in utroque latere prope marginem confluentibus petiolo glabro canaliculato 5-10 mm. longo. Inflorescentiae masculae plerumque 3- vel 5-florigerae binae in axillis foliorum pedunculis bracteatis 10-14 mm. longis pedicellis ca. 5 mm. longis. Flores rotati ca.

Figure 174. *Mollinedia stipitata*

2 mm. in diam. tepalis 4 glabris 2 interioribus laciniose appendiculatis staminibus ca. 26 1.0-1.5 mm. longis antheris hippocrepiformibus. Inflorescentiae femineae plerumque uniflorae solitariae vel binae in axillis foliorum pedunculis bracteatis ca. 8 mm. longis pedicellis bracteolatis ca. 10 mm. longis. Flores ca. 4 mm. in diam. glabri tepalis 4 ca. 2 mm. longis mox deciduis carpellis ca. 20 separatis stylis longis. Receptacula fructifera disciformia repanda 7-15 mm. lata pedunculo cum pedicello 10-45 mm. longo drupis stipitatis fuscis striatis ellipsoideis mucronatis 16-20 mm. longis ca. 10 mm. latis basem attenuatis.

CHIRIQUÍ: between the R. Ladrillo and Los Siguas, southern slope of Cerro de la Horqueta, 1200-1700 m., *Pittier* 3280 (HOLOTYPE, NY); cloud forest, Cerro Horqueta, 6500 ft., *Von Hagen & Von Hagen 2064;* humid forest between Alto de las Palmas and top of Cerro de la Horqueta, 2100-2268 m., *Pittier* 3262.

Among North American species this seems most closely related to a specimen from Chiapas (*Matuda 442*) determined by Standley as *M. viridiflora* Tul. Standley's determination is doubtful, however, because a photograph of the type of *M. viridiflora* alarmingly resembles what is currently passing as *M. guatemalensis* Perk., a species with large pergameneous leaves, the staminate flowers 5-8 mm. in diameter at anthesis, with 30-48 stamens and with large short-stipitate drupes. Although Perkins has stated that the stamens in *M. viridiflora* are "usque 24," this seems to

be the only character separating it from *M. guatemalensis*. The new species is readily distinguished by its small narrow leaves, the small male flowers, and the long-stipitate, apically mucronate, basally attenuate drupes.

The Von Hagen specimen poses an interesting problem as it consists of both staminate and carpellate branches. Their data say "tree, 8 ft tall." By the singular usage of tree, we would be forced to conclude that the species is sometimes monoecious, but until the physical connection of male and female flowers is verified, this is pure speculation. There are no reports of monoecism in *Mollinedia*, but the condition is not uncommon in *Siparuna*.

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(PIPERACEAE - MONIMIACEAE)

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